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THE CALCAREOUS GRASSLANDS OF THE CARBONIFEROUS AND OOLITIC LIMESTONES OF SOUTH-WEST ENGLAND: a comparative study with special reference to edaphic conditions.

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CONTENTS

I. Introduction

Detailed studies of calcareous grassland in Britain have been made mostly on the Chalk. The grasslands of other limestones have received much less attention and few detailed accounts have been published. Of these other limestones, the Carboniferous Limestone and Jurassic Oolitic Limestone formations have by far the most extensive outcrops, and are the only ones bearing sizable tracts of semi-natural grassland.

The grasslands of the Carboniferous Limestone were characterized and briefly described in a number of district surveys made at the beginning of the present century. Thus, calcareous grassland was described from upland slopes in West Yorkshire (Smith and Rankin, 1903), from the scars and fells of the Northern Pennines (Lewis, 1904), from limestone slopes in Western Ireland (Vegetation Committee, 1908), and from the limestone dales of the Peak District, Derbyshire (Moss, 1913). More recent studies of Carboniferous Limestone grassland have been made by McLean (1935) in South Wales, Praeger (1934) and Webb (1947) in West Ireland, and by Balme (1953) in the Derbyshire Dales. The pastures of the

Carboniferous Limestone in the Mendip Hills, Somerset have been only very briefly described by Moss (1907).

The salient points about the character of grassland found on Carboniferous Limestone emerging from these studies may be summarized in the following statements: a typical calcareous community, similar to Chalk grassland, is restricted to situations where the soil is shallow above the rock, e.g. on many of the steeper slopes; where the soil is deeper e.g. on level or gently sloping ground, calcium carbonate is lost by leaching from the surface layers, and a non-calcareous flora develops; with further increase in soil-depth and progressive leaching, a limestone heath community is established, consisting of typical calcareous species growing in close association with plants characteristic of heath-vegetation; the tendency for a soil of low base-content, supporting heath-like vegetation, to develop over Carboniferous Limestone is more pronounced in the wetter and cooler parts of the British Isles, and reaches an extreme condition in Ireland, where peat is formed in contact with the solid limestone rock.

Thus the readiness with which Carboniferous Limestone soils lose much of their exchangeable bases limits the extent of occurrence of calcareous grassland, and leads to peculiarities of its floristic composition.

Studies of grassland on the Jurassic Oolitic Limestone (which is referred to subsequently as 'the Oolite' or 'Oolitic Limestone') have been brief and, in the main, superficial. Among the accounts more directly concerned with the occurrence of the rarer plants on this limestone, may be mentioned Riddelsdell (1921), who briefly reviews the flora of the Gloucestershire oolite and gives lists of the more important calcicole plants occurring there, Druce (1930), who gives lists of plants growing on old, grass-covered quarries in Northamptonshire, and Lousley (1950), who gives a general account of the rarer characteristic plants of the Oolite.

Accounts with a more ecological bearing are given by Horwood and Gainsborough (1933), for the scattered areas of Oolitic grassland in Rutland and Leicestershire, and by Price (1948) for the grasslands of Gloucestershire. Hepburn (1942) has made a detailed study of the limestone grassland occurring in an old stone quarry on the Northamptonshire oolite.

The resemblance of the calcareous grasslands of the Oolite to those of the Chalk is indicated in a number of these accounts; a similarity in appearance and composition is also noted by Moss (1907), Tansley and Adamson (1913), Tansley (1939) and Salisbury (1952). Moss (1907), and Price (1948) state further that, in Somerset and Gloucestershire, the Oolitic Limestone grassland can scarcely be distinguished from that occurring on Carboniferous Limestone.

Among other general points noted in these accounts, may be mentioned: the frequent dominance of the taller grasses, *Zerna erecta* and *Brachypodium pinnatum* on the Oolite, especially where grazing is less intense, and the slightly greater depth of soil on this limestone as compared with the Chalk, possibly because the less pure Oolitic rock gives rise to more residual material on weathering.

Thus, apart from recognizing a similarity to the Chalk grassland, no detailed characterization of the calcareous grasslands of the Oolite has yet been made.

In view of the scant information available on the composition of Oolitic grassland, and also, to a lesser extent, on that of Carboniferous Limestone grassland (especially in south-west England), a detailed study of both these types was undertaken in the Bristol area. Throughout the study, emphasis was placed on the comparison of the calcareous grasslands occurring on the two limestone formations, thus giving valuable insight into the problems of occurrence and distribution of species on calcareous substrates. A three-cornered comparison, including Chalk data as well, would have furthered this purpose, but this was not the direct concern of the present investigation.

Taking into account the geographical proximity of outcrop of the two rock formations in the Bristol region, there seemed a high probability that climatic conditions on these formations would be essentially similar and thus, comparative inferences could more confidently be related to other factors of environment. Of these, particular attention was focussed on the properties of the soil, and an analytical survey of soils from calcareous grassland in varied situations on the two rock formations was pursued in conjunction with the study of the vegetation.

In the light of information obtained about the distribution and relative abundance of the component species of the two series of grasslands, an experimental attempt was made to assess the importance of differences in soil properties on Oolitic and Carboniferous limestones in determining the existing differences of floristic composition. This experiment was, of necessity, preliminary in nature, but the results gave some indication of the growth-rates of a number of selected species in the two soil-types.

Phot. 1. The southern face of the Mendip Hills; Wavering Down and Winscombe Hill. The rough grazings on the slopes consist of calcareous grassland with gradations to limestone heath and scrub.

Phot. 2. The Cotswold escarpment at Stinchcombe Hill, one of the few places where the escarpment slopes bear calcareous grassland.

II. Topography and general physiognomy of the limestone country surveyed in the present investigation.

In south-west England the Carboniferous and Oolitic Limestones form prominent features of the landscape, since their main outcrops occur respectively in the upland regions comprising the Mendip and Cotswold Hills (Fig.1, p:8).

The Mendip Hills, composed predominantly of massive - bedded Carboniferous Limestone, extend westwards from Frome to Brean Down on the coast. The limestone rises steeply from the surrounding country (Phot.1) and then levels out to a gently undulating, upland plateau, more than 5 miles broad at its widest, and rising to over 900 feet in several places. The plateau is sculptured by several dry-floored valleys, with sides often very steep and rocky.

Mendip country (Phot.1; Phot.3, p.9) is characteristically very windswept, and has a typically upland climate. There are few trees except for the small areas of woodland scattered mainly on the escarpment slopes. The land-surface is marked by frequent outcrops of bare limestone rock, in the form of rugged crags and weathered rock-fragments projecting through the thin soil.

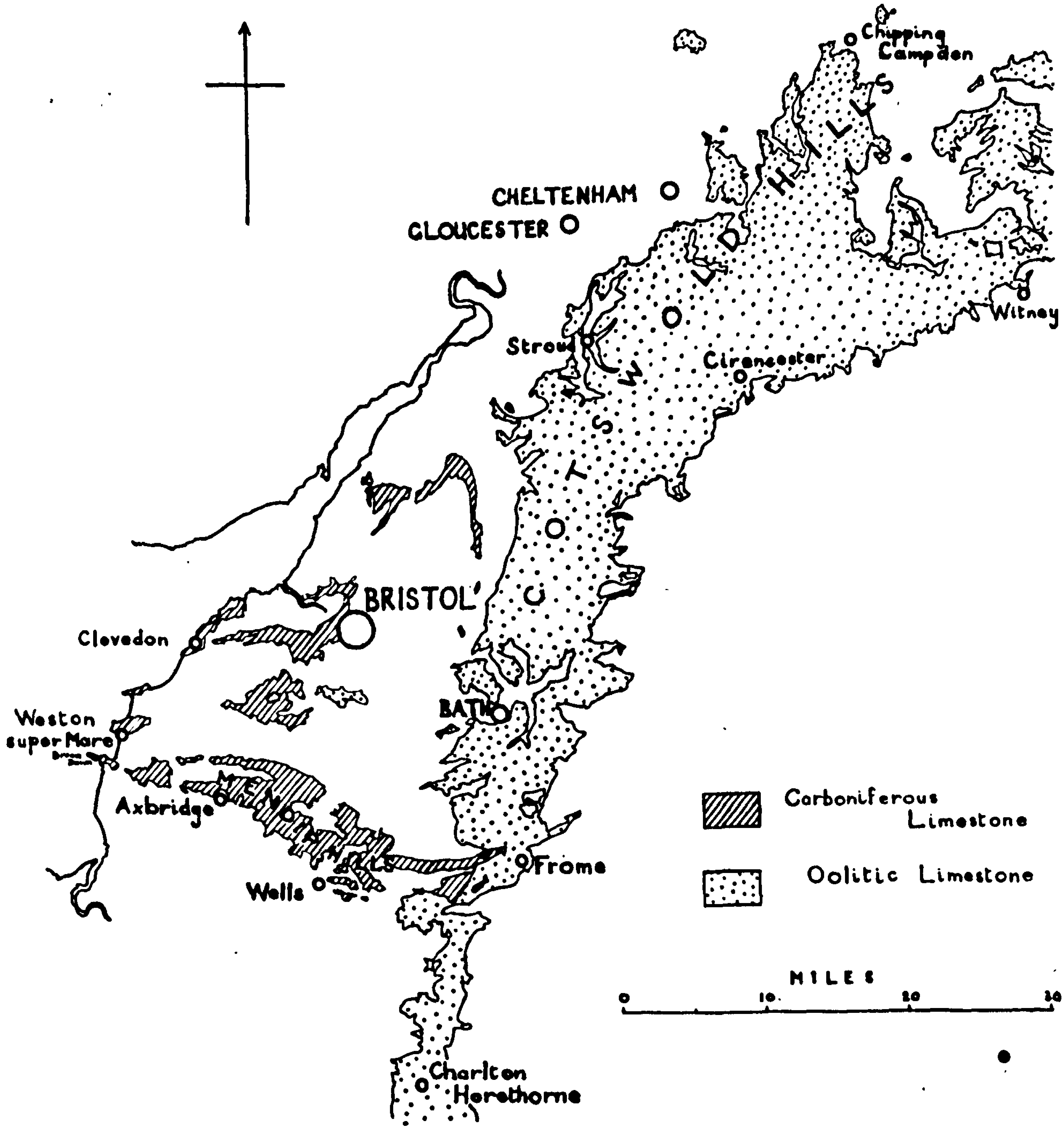


Figure 1. Sketch-map showing the outcrops of Carboniferous and Oolitic Limestones in the area surveyed in the present investigation.

The plateau is largely under cultivation, but there are considerable areas of rough grazings; on the Carboniferous Limestone, these are mainly bracken-infested pastures, often associated with scrub-vegetation, of Hawthorn (Crataegus monogyna), Gorse (Ulex gallii), or Bramble (Rubus spp.). Bracken (Pteridium aquilinum) is the predominant plant, except in areas heavily grazed or with shallow soil, which then carry open grassland. Limestone heath vegetation occurs locally.

On the limestone slopes, the rough grazings are similar but, in general, are more grassy.

North of the Mendips, Carboniferous Limestone outcrops in a number of regions in the country flanking the Severn Estuary, and here forms irregular areas of moderately elevated land. These outcrops carry mainly woodlands where the land is uncultivated, but there are occasional small areas of rough grazings.

The Oolitic Limestone outcrops in a more orderly fashion, and forms a great inland belt running roughly parallel to the lower part of the river Severn. The greater part of this outcrop forms the mass of the Cotswold Hills, extending

Phot. 3. Crook Peak (centre) and Wavering Down (right), at the western end of the Mendips. The Carboniferous Limestone shows through the soil in many places on the southern slope at the right of the photograph.

Phot. 4. A dry-floored valley on the Cotswold plateau, at Barnsley Wold, near Cirencester. The valley sides in the middle distance bear calcareous grassland. The vegetation on the gentle slope in the immediate foreground is a rare example of leached grassland on Oolite.

from the Avon valley at Bath northwards to Stroud, and thence, north-eastwards to Chipping Campden (Fig.1, p.8).

The Cotswolds, while emerging less abruptly than the Mendips, rise rather steeply from the Vale of the Severn (Phot.2, p:7) and reach a maximum height of 1,083 feet at Cleeve Hill, Near Cheltenham. The general height of the range gradually decreases southwards to Bath, where the hills attain an altitude of between 600 and 780 feet.

Except for a short distance in its southern part, the face of the escarpment is greatly indented by ramifying valleys, from which streams arise and flow into the Severn. East of the escarpment the Cotswolds form an expansive tableland 10 to 20 miles broad, an undulating plateau, much intersected by deep valleys in the north-west, less frequently so in the south-east. The general level of the land slopes very gradually south-eastwards, following the dip of the limestone rock, until the Oolite finally abuts on the Cornbrash.

The Cotswold country east of the escarpment is typically open (Phot.4) and exposed to winds, which however, seem less severe than on the Mendips. Much of the escarpment and many of the valleys are wooded, but elsewhere only scattered groups of trees occur. The plateau is extensively cultivated, the well-drained, stony soil being very suitable for corn-growing. On the steeper, tree-less slopes a form of downland occurs, which becomes conspicuously coarse if left ungrazed. On the higher ground in the North Cotswolds, there are areas of rough grazings, covered mainly with coarse downland and Hawthorn-scrub.

The Oolitic Limestone forms hills and slopes with a contour less harsh than the Carboniferous Limestone, and the parent rock is almost everywhere covered with a moderately thick layer of soil.

North-east of the Cotswolds the outcrop of the Oolite becomes less conspicuously elevated and, passing into the Midlands, it gradually merges with the surrounding country. The land here is mainly agricultural, but there are a few uncultivated areas.

South of Bath, the Oolite outcrop reaches the general height of 450 to 600 feet, but is deeply dissected by branching valleys, carrying tributaries of the Avon. Strata of the Fuller's Earth formation outcrop extensively on the steep slopes of these valleys, but sizable outcrops of limestone are rarely encountered.

In the Frome region the Oolite country merges with the eastern end of the Mendips and Carboniferous and Oolitic Limestones outcrop side by side.

South of Frome, the Oolite outcrops as a narrow belt, producing a steep western escarpment in places. In this region the land-surface is intersected by numerous streams and small rivers, and is of very irregular contour. The few unploughed slopes in this predominantly agricultural area very rarely occur on typical limestone, which is here of extremely limited occurrence.

Phot. 5. Calcareous grassland on a south-west slope on Carboniferous Limestone (Winscombe Hill). Yews growing on the screes of this slope are severely cut by the wind.

Phot. 6. A grazed slope bearing calcareous grassland on the Oolite, near Tetbury.

III. Description of the semi-natural calcareous grasslands occurring on the Carboniferous and Oolitic Limestones.

1. Distribution of these grasslands.

In order to compare the semi-natural calcareous grasslands developed on the Carboniferous and Oolitic Limestones, stretches of undisturbed grassland were sought over these two formations. In view of the preliminary nature of this investigation, areas containing calcareous grassland were looked for over a wide extent of country on each limestone. Thus, most of the Carboniferous Limestone outcrops of the Bristol region were scrutinized fairly exhaustively, while the search on the Oolite was extended from Charlton Hawthorne, in south-east Somerset, to Minster Lovell, Near Witney, in Oxfordshire. Although calcareous grassland is present on the Oolite outcropping north-east of the Cotswolds, the northern limit of survey in this investigation was arbitrarily placed near the Gloucestershire - Oxfordshire border, mainly because, in this region, local conditions, such as those of climate, geology or of past history of the vegetation, begin to differ appreciably from those typical of the Cotswold country.

Referring to the geological map (p.8.), comparison of the two types of grassland would seem to have been best made in the Frome area. However, it was early observed that there were practically no areas of calcareous grassland, suitable for recording, on the Oolite south of Bath, and very few on the Carboniferous Limestone east of Wells, and that, in fact, the centres of distribution of the two types were in the Cotswold and Mendip Hills respectively.

Owing to the intensive agricultural programme carried out during and since the war, only small areas of pasture-land remain undisturbed. These are to be found mainly on the steeper slopes and in tracts of rough grazings.

On the Oolite the steeply-sloping sides of valleys often carry undisturbed grassland over limestone, but in very many valleys a limestone vegetation is not extensively developed, because the slopes consist mainly of clay outcrops with only limited amounts of limestone. This situation is of widespread occurrence near the escarpment, but further east on the gentle dip-slopes, the sides of valleys are mainly of limestone, and often carry undisturbed grassland. Undisturbed pasture-land on level or gently-sloping sites is of extremely rare occurrence on the Oolite and is found mainly in the rough grazings on high ground in the North Cotswolds.

On the Carboniferous Limestone undisturbed pasture-land is less rigidly confined to the steep slopes; the thin layer of soil and the exposed situations characteristic of extensive outcrops of this rock-formation make much of the land unsuitable for intensive farming and large areas are used as rough grazings. However, most of the land in this category on level or gently-sloping ground is clothed with Bracken, associated with Bramble, and Gorse-or Hawthorn-scrub; alternatively, in some places, a limestone heath vegetation predominates. Only where the soil is very shallow or where grazing is heavy, is there found a type of grassland with the familiar calcicolous species. These conditions occasionally prevail on the flatter regions but are, in general, more characteristic of the steeper slopes.

2. <u>Selection of areas for recording</u>

Sites were chosen to represent a wide range of environmental conditions on each limestone, but, while maintaining this variety of habitat, attempts were directed, as far as possible, to obtain records from situations with corresponding site-characters for the two limestone formations. For example, having recorded a number of steeply-sloping sites on the Carboniferous Limestone, an equivalent number of sites, broadly comparable in steepness to these, were recorded on the Oolitic Limestone. The depth of soil, degree of exposure to wind, aspect, and intensity of grazing were other site-characters considered. This precaution in the selection of sites for recording ensured that the vegetation-data, when finally aggregated for each limestone, were on a reasonable basis for comparison.

Areas for recording, approximately 1/4 to 1 acre in size, were roughly delimited in uniform stretches of grassland, that bore no evident signs of secondary status. Apart from any obvious signs of disturbance within the past few years, and short of assurance from the owner of the land, evidence of interference could generally be obtained by superficial inspection of the appearance and botanical composition of the vegetation. The presence of considerable numbers of arable weeds, an abundance of agricultural plants, such as ley-grasses, or of woodland plants were regarded as strong indications of abnormal treatment.

3. Method of recording the vegetation.

Since descriptions of the vegetation cover were to be obtained from a large number of different situations over a wide geographical area on each limestone-formation, a rapid method of recording was necessary. For this reason, the method of subjective estimation was preferred to a more objective method, and was adopted as a routine procedure in the present investigation.

The subjective method has been widely used in primary surveys of vegetation, e.g. Moss (1907), Tansley and Adamson (1926), and to some extent for detailed studies, e.g. Cornish (1954). It has the advantage of allowing the collection of large amounts of vegetation-data over a wide area in a comparatively short time, and it is suitable for recording the more perceptible features of floristic composition. However, as shown by Hope-Simpson (1940), the results obtained by the subjective method exhibit considerable variation under different conditions of recording. Thus results are likely to be different for the same area recorded by separate observers, or by the same observer at different seasons of the year. For the present investigation the effect of errors inherent in the subjective method was reduced to a minimum, since the vegetation-data from the two types of calcareous grassland were obtained under closely similar conditions of recording, and, further, were to be analysed on a comparative basis.

About half of the vegetation records were made from sites visited during Autumn 1952 and the remainder were obtained during the late summer and autumn of 1953. Since most of the vegetation records were obtained in late summer or early autumn, the possibility arises that some of the less abundant plants conspicuous only in spring may have been overlooked or assigned a low frequency-estimate. Data obtained from sites revisited in the spring showed no serious disagreement when compared with records made in the autumn.

The mode of recording the vegetation-cover of a selected area followed that of Hope-Simpson (1940 and unpublished data).

Before listing the species on an area and estimating their relative abundance, brief field-notes were made on general site-characters, the nature of the soil and on the appearance of the plant cover; summaries of these observations are included in the accounts of physiognomy and of the environmental factors(p.20; p.52.).

The manner of listing the flora was straightforward: a list was made of all the species observed during an inspection of 2-3 square yards of turf, near the middle of the area delimited for recording. Similar close inspections of the turf were made at a number of scattered points over the area, until additional species were no longer encountered.

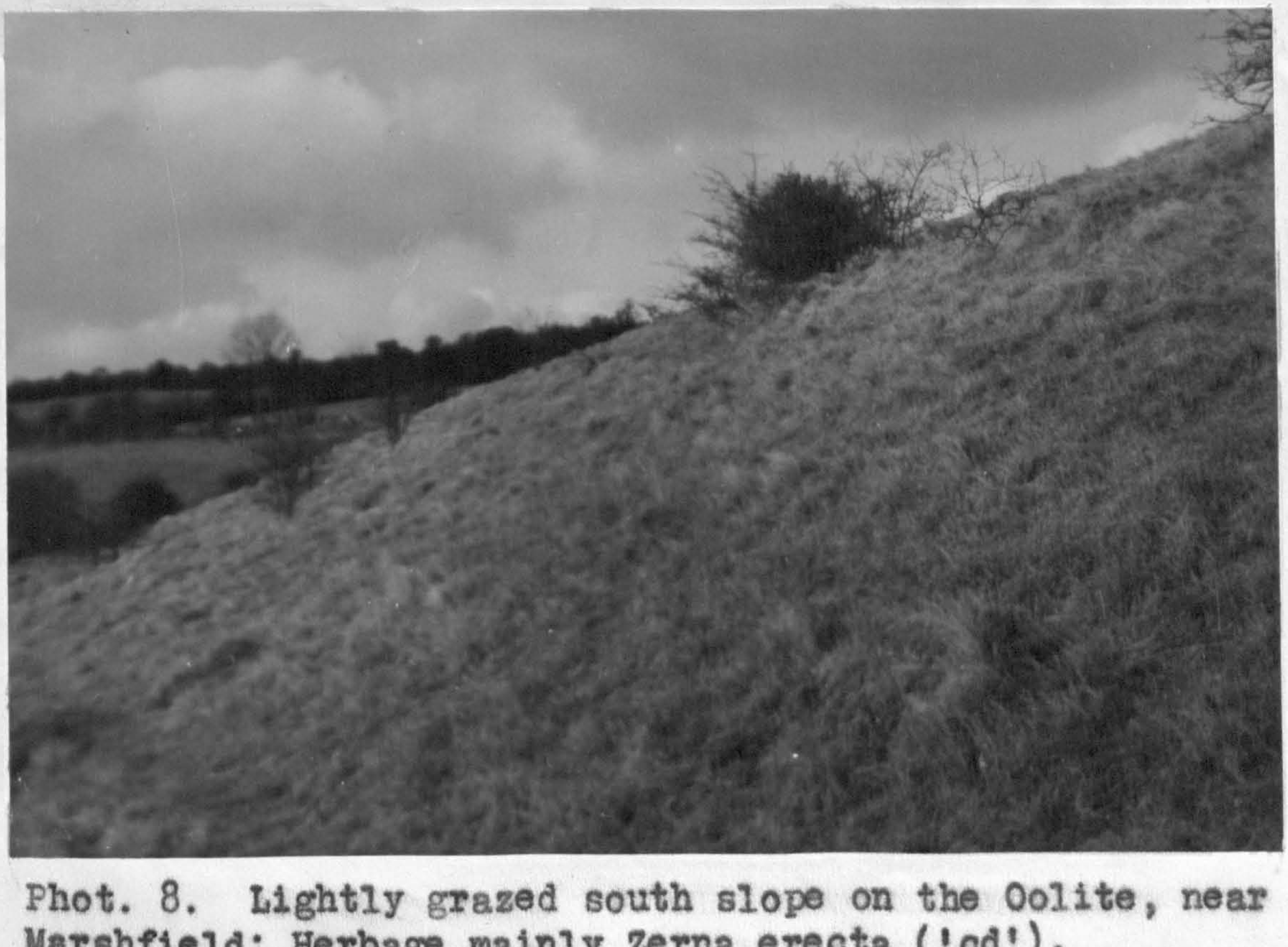
The significance of the categories of relative abundance was similar to that denoted by other workers; thus the categories 'dominant' (abbreviated 'd'), 'co-dominant' (cd), 'very abundant' (va), 'abundant' (a), 'frequent' (f), 'occasional' (o), 'rare' (r) were used to designate decreasing amounts of relative abundance. An estimate of 'dominant' was only given when the sub-aerial parts of a single species completely smothered the remaining components of the herbage over the whole of the recorded area. 'Co-dominant' was given where two species shared dominance of an area, or where a single species occupied at least half of the vegetation-cover; 'rare' implied species occurring only once or a small number of times over the whole area. The other categories of relative abundance were graded between 'co-dominant' and 'rare' in accordance with purely subjective standards.

4. Observations and results.

a) Physiognomy

The calcareous grasslands of the Carboniferous and Oolitic limestones in south-west England exhibit physiognomic features commonly associated with turf developed on a calcareous substratum; thus on both limestones there is a more or less closed community, essentially of low stature and consisting of dicotyledons, grasses and mosses in varying proportions, with the plants often showing signs of reduced vigour. Under the influence of heavy grazing an extremely short and closed turf, dominated by the smaller grasses or rosette herbs is developed. Mosses from a conspicuous part of the vegetation only on the moister sites, commonly those with a northerly aspect, and lichens only assume importance on the drier, more exposed

Phot. 7. Moderately grazed calcareous grassland on a gentle south slope on the Carboniferous Limestone at Goblin Combe, Cleeve. The herbage here is extremely short.



Phot. 8. Lightly grazed south slope on the Oolite, near Marshfield; Herbage mainly <u>Zerna erecta</u> ('od').

sites with very short turf.

However, there are striking physiognomic differences between the two varieties of grassland: the majority of sites on the Carboniferous Limestone have a short, closed turf - a mosaic of dwarfed herbs and grasses; a few areas are clothed with a taller vegetation dominated usually by Fescues (Festuca rubra and F. ovina), very occasionally by other tall-growing grasses. On the other hand, a large number of the calcareous grassland sites on the Oolitic limestone have a taller and more open turf, dominated by coarser grasses (chiefly Zerna erecta and Brachypodium pinnatum), giving an entirely different appearance to the vegetation. (Phot.7,8.)

Where the turf has been subject to regular grazing there is a less marked difference of physiognomy, but the more open turf and the greater luxuriance of the plants on the Oolitic Limestone was almost always noticeable. Only one stretch of grassland encountered on the Carboniferous Limestone had a facies indistinguishable from that commonly found on the Oolite.

Summaries of field-notes on the appearance of the

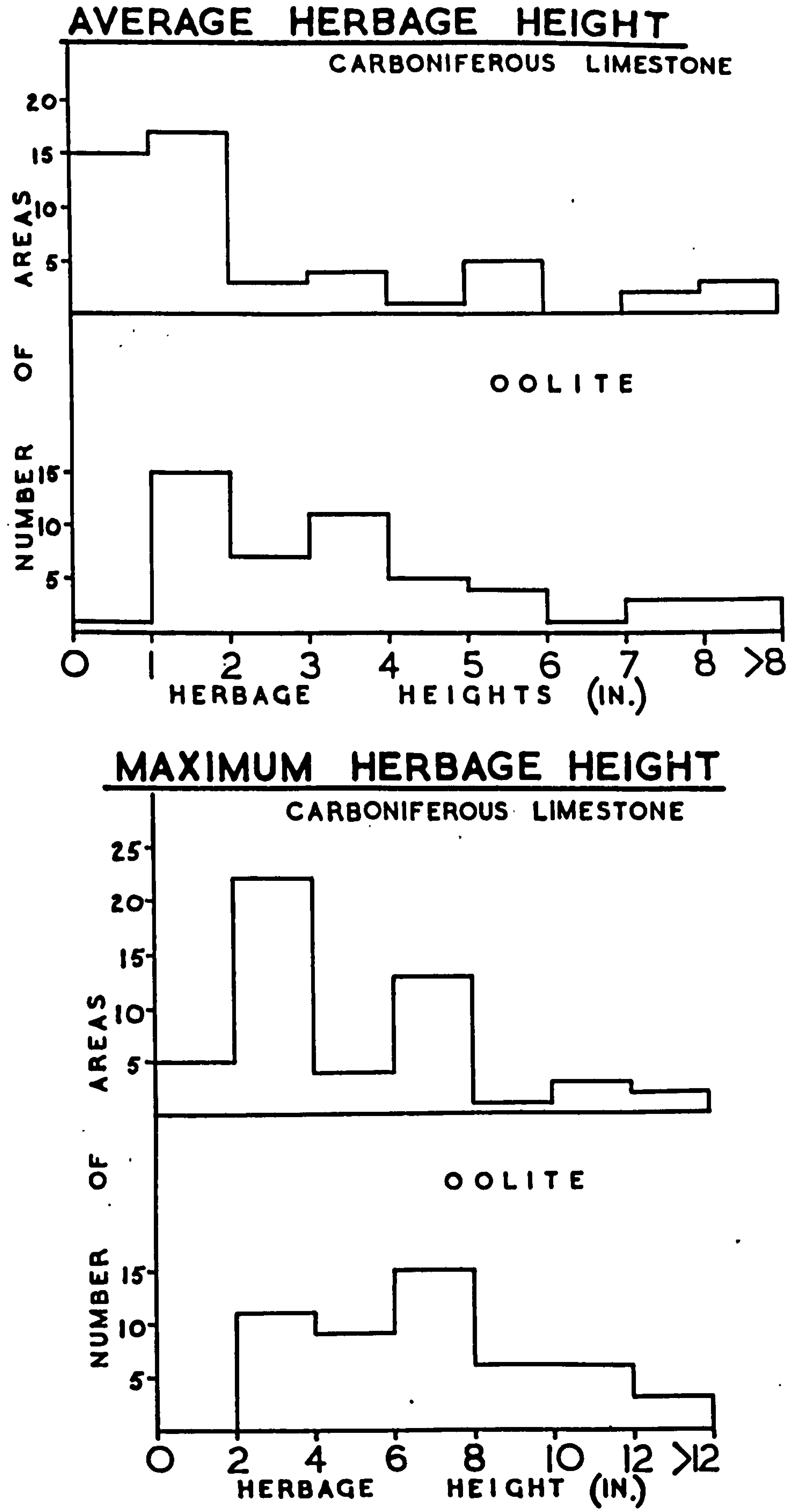


Figure 2. Comparison of the herbage heights in calcareous grassland on the two limestones.

vegetation made for each area recorded show the following general features:-

Though both types commonly carried a few scattered inflorescences of some of the component species, the Oolitic grassland more frequently had large number of grass inflorescences, while that of the Carboniferous Limestone often showed a more extensive flowering of dicotyledons.

Measurements of the maximum and apparent average heights of the herbage on each area confirm the general observation that the Oolitic limestone carries a taller vegetation. The extent of this difference in height, can be judged from the accompanying histograms, based on measurements from 50 areas on each limestone.(Fig.2).

It may be seen that, although both limestones often carry grassland with a short herbage, the average height is much more frequently very short on the Carboniferous Limestone, whereas it is more often moderate or tall on the Oolite.

In addition to the direct effects of differences in environmental conditions operative on the two grasslands at the present time, the difference in form of the vegetation-cover undoubtedly arises to a large extent from very

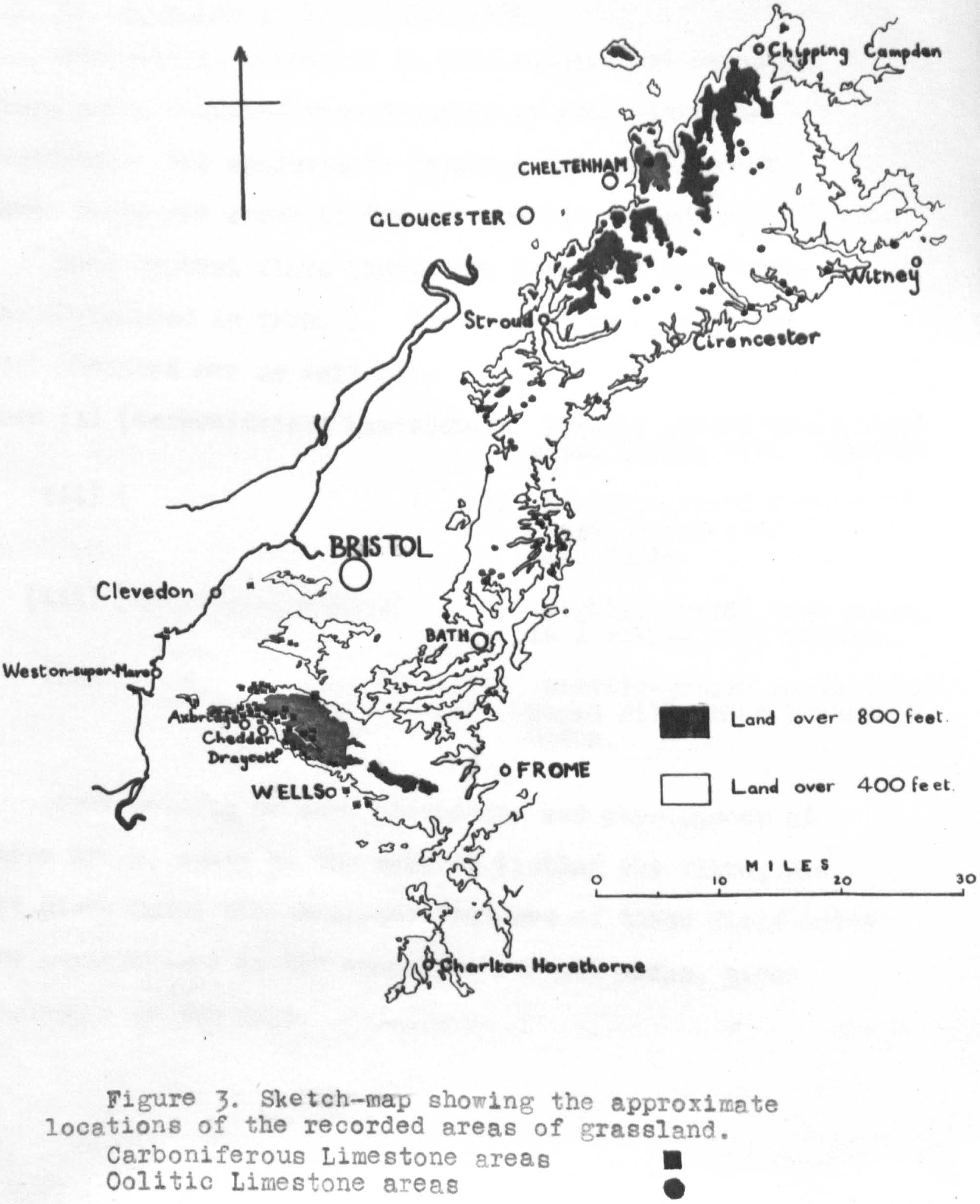


Figure 3. Sketch-map showing the approximate locations of the recorded areas of grassland.
Carboniferous Limestone areas ■
Oolitic Limestone areas ●

general differences in floristic composition. These will now be considered in detail.

b) Analysis of the flora lists

The results discussed in this section are based on flora lists compiled from 50 areas on each limestone territory. The approximate geographical positions of these areas are shown in the accompanying sketch map (Fig.3).

Four typical flora lists, two from each limestone, are reproduced in Table 1. The areas from which these were obtained are as follows:-

Area (i) (Carboniferous Limestone):	lightly grazed south slope, Shute Shelve Hill, Axbridge.
(ii) (" "):	heavily-grazed south-east slope, Worminster Sleight, near Wells.
(iii) (Oolitic Limestone) :	lightly-grazed west slope, in a valley near Tresham.
(iv) (" ") :	heavily-grazed south slope, Broad Hill, near Hawkesbury Upton.

Full details of site-characters and physiognomy of these areas, noted at the time of listing the flora, are not given here; the important features of these field-notes are incorporated in the summaries for all areas, given elsewhere in the text.

The nomenclature of Clapham, Tutin, & Warburg (1952) was used for angiosperms. For mosses, liverworts and lichens, the handbooks of Dixon, (1924) McVicar, (1912), and Smith (1921) were used for identification, and the names given by these authors have been retained for most species.

TABLE I.

	(i)	(ii)	(iii)	(iv)
Achillea millefolium	-	-	-	o.lf
Agrostis stolonifera	-	-	o	-
" tenuis	f	a	o	-
Anthoxanthum odoratum	r	o	-	-
Anthyllis vulneraria	-	-	r	-
Asperula cynanchica	-	-	r	-
Bellis perennis	-	f	-	-
Blackstonia perfoliata	-	-	f	-
Brachypodium pinnatum	-	-	r.ld	-
" sylvaticum	o	-	-	-
Briza media	f-a	f	f	a
Campanula glomerata	-	-	f	-
" rotundifolia	-	-	o	-
Carex caryophyllea	a	a	f	-
" flacca	va	a	a	a
Carlina vulgaris	r	r	o	-
Centaurea nigra	-	o	o	-
" scabiosa	-	-	r	-

(contd.)

(Table I. contd.)

	(i)	(ii)	(iii)	(iv)
Centaurium minus	r	-	-	-
Chrysanthemum leucanthemum	-	o	-	-
Cirsium acaule	f	f	a-va	f
* Crataegus monogyna	r	-	r	f
Cynosurus cristatus	-	f	-	r
Dactylis glomerata	-	r	r	o
Euphrasia nemorosa	-	f	f	-
Festuca arundinacea	-	r	-	-
" ovina	cd	f	a	cd
" rubra	r	f-a	-	-
Filipendula vulgaris	a	-	-	-
* Fraxinus excelsior	r	-	o	-
Galium mollugo	r	-	-	r
" verum	a	o	o	r
Gentianella amarella	-	-	o	-
Helianthemum chamaecistus	a	f-a	a	f
Helictotrichon pratense	a	a	r	f-a
" pubescens	-	-	-	r
Hieracium pilosella	o	a	a	a-va
Hippocrepis comosa	-	-	o	-
Hypochaeris radicata	-	f	-	-
Koeleria gracilis	a	f-a	f	a
Lathyrus pratensis	-	-	-	o

(contd.)

(Table I. contd.)

	(i)	(ii)	(iii)	(iv)
Leontodon hispidus	-	f	a	r
" leysseri	o	f	-	o.lf
Linum catharticum	o	f	f	f
Lotus corniculatus	a	a	f	f-a
Luzula campestris	o	-	-	-
Medicago lupulina	-	f	-	a
Ononis repens	-	-	r	-
Orchis fuchsii	-	-	r	-
Picris hieracioides	-	-	r	-
Pimpinella saxifraga	-	o	o	-
Plantago lanceolata	f	a	f	o
" media	-	f	o	o
Poa pratensis	-	-	r	o
Potentilla erecta	-	r.lf	-	-
" reptans	f	-	-	-
Poterium sanguisorba	va	va	a	f
Primula veris	-	o	o	-
Prunella vulgaris	o	f	o	o
* Quercus robur	-	-	f	-
Ranunculus bulbosus	r	f	r	a
Scabiosa columbaria	r	f	o	o
Senecio jacobaea	-	-	-	r
Serratula tinctoria	-	-	r	-

(contd.)

(Table I. contd.)

	(i)	(ii)	(iii)	(iv)
Sieglingia decumbens	o	a.lva	r	-
Stachys officinalis	-	o	-	-
Succisa pratensis	-	f.la	f-a	-
Taraxacum officinalis	o	-	-	r
Thymus drucei	a	f-a	f-a	a
Trifolium pratense	o	f	-	f
" repens	-	o	r	a
Veronica officinalis	r	-	-	-
Viola hirta	-	f	f	-
Zerna erecta	-	-	cd	va
<u>Mosses and lichens</u>				
Acrocladium cuspidatum	-	o	f	-
Brachythecium rutabulum	-	f	o	-
Barbula unguiculata	-	-	f	r
Camptothecium lutescens	-	-	-	r
Cladonia rangiformis	o	-	o	-
Dicranum scoparium	o	-	-	-
Eurhynchium praelongum	-	f	f	o
Fissidens taxifolius	r	f	a	o
Hypnum cupressiforme	o	f	f	o
" molluscum	-	f	a	f
Mnium undulatum	r	-	-	-
Pseudoscleropodium purum	o	f	f	f

Shrub - and tree - species were recorded only when forming part of the herbage.

50 such lists from each limestone were arranged in a composite table, from which were obtained, for every species, the total frequency of occurrence, and the number of times the various levels of relative abundance were reached. These summarizing totals for the two limestones are set out in Tables 2-6, where species are classified according to their relative behaviour in the two series of grasslands. In these tables and in the discussions following, references to the occurrence or absence of a species on one or other of the limestone-formations apply only to the observed behaviour of that species on the hundred areas of grassland from which the data in Tables 2-6 were obtained, and are not intended to denote its behaviour over the whole area of outcrop of each limestone. Thus 'Species found only on the Carboniferous Limestone' (Table 5) includes some species e.g. Pteridium aquilinum, known to be present on the Oolite but which did not occur on any of the fifty Oolite areas recorded.

TABLE 2

Species with more frequent occurrence on the Carboniferous Limestone.

a) with similar levels of abundance on the two limestones:

	Carboniferous Limestone								Oolitic Limestone							
	Number of times recorded as:							Total occurrences	Number of times recorded as:							Total occurrences
Abundance classes:	d	cd	va	a	f	o	r		d	cd	va	a	f	o	r	
Senecio jacobaea	.	.	.	.	9	15	6	30	.	.	.	.	2	6	6	14
Anthoxanthum odoratum	.	.	1	2	12	9	3	27	.	.	.	1	6	5	1	13
Hypochaeris radicata	.	.	.	1	4	13	9	27	.	.	.	.	3	10	1	14
Polygala vulgaris	.	.	.	.	4	11	11	26	.	.	.	.	2	4	7	13
Carlina vulgaris	.	.	.	1	5	11	7	24	.	.	.	.	2	2	6	10
Lichen																
Cladonia pyxidata	.	.	.	.	1	7	5	13	.	.	.	.	1	2	5	8

b) with greater levels of abundance on the Carboniferous Limestone:

	d	cd	va	a	f	o	r	Total occurrences	d	cd	va	a	f	o	r	Total occurrences
Thymus druoei	.	.	8	23	17	1	1	50	.	.	.	12	12	12	1	37
Koeleria gracilis	.	.	8	25	11	1	2	47	.	.	.	5	15	2	8	30
Agrostis tenuis	.	.	7	21	14	5	1	47	.	.	1	1	5	17	4	28
Carex caryophyllea	.	.	7	22	11	6	1	47	.	.	.	3	11	12	6	32
Sieglingia decumbens	.	.	5	13	16	9	3	46	.	.	.	2	1	.	4	7
Helictotrichon pratense	.	.	1	15	16	6	4	42	.	.	.	2	11	9	10	32
Leontodon leysseri	.	.	2	4	10	9	7	32	.	.	.	1	1	2	4	8

(contd.)

Table 2b (contd.)

Abundance classes:	d	cd	va	a	f	o	r	Total	d	cd	va	a	f	o	r	Total
Euphrasia nemorosa	.	.	.	3	14	7	5	29	.	.	.	.	5	3	1	9
Potentilla erecta	.	.	1	4	6	6	5	22	.	.	.	.	2	3	1	6
Veronica officinalis	.	.	.	.	5	6	11	22	.	.	.	.	1	.	1	2
Centaurium minus	.	.	.	2	5	12	2	21	.	.	.	.	1	6	7	14
Fragaria vesca	.	.	.	1	8	10	2	21	.	.	.	.	.	4	3	7
Viola riviniana	.	.	.	1	9	2	4	16	.	.	.	.	2	1	1	4
Cirsium palustre	.	.	.	.	1	6	6	13	.	.	.	.	.	1	2	3
Brachypodium sylvaticum	.	.	.	.	1	6	5	12	.	.	.	.	.	1	1	2
Teucrium scorodonia	.	.	.	.	3	4	4	11	.	.	.	.	.	.	1	1
Spiranthes spiralis	.	.	.	.	2	2	4	8	.	.	.	.	.	.	1	1
Mosses and Lichens																
Dicranum scoparium	.	.	.	7	18	7	2	34	.	.	.	1	2	2	2	7
Hypnum cupressiforme	.	.	.	2	13	14	2	31	.	.	.	.	1	4	1	6
Cladonia rangiformis	.	.	.	1	10	7	7	25	.	.	.	.	.	5	3	8
" furcata	.	.	.	1	1	6	3	11	.	.	.	.	.	1	.	1

TABLE 3

Species with more frequent occurrence on the Oolitic Limestone.

a) species with similar levels of abundance on the two limestones:

	Carboniferous Limestone								Oolitic Limestone							
	Number of times recorded as:							Total occurrences	Number of times recorded as:							Total occurrences
Abundance classes:	d	cd	va	a	f	o	r		d	cd	va	a	f	o	r	
Plantago media	.	.	.	.	3	3	1	7	.	.	.	1	17	14	6	38
Trifolium repens	.	.	.	4	6	6	3	19	.	.	1	3	9	18	1	32
Cynosurus cristatus	.	.	.	4	8	.	2	14	.	.	1	3	11	13	3	31
Pimpinella saxifraga	.	.	.	.	1	4	4	9	.	.	.	.	5	15	5	25
Crataegus monogyna	.	.	.	.	.	2	9	11	.	.	.	.	.	8	10	18
Phleum nodosum	.	.	.	.	.	2	1	3	.	.	.	.	1	11	5	17
Blackstonia perfoliata	.	.	.	1	3	4	.	8	.	.	.	.	8	3	5	16
Chrysanthemum leucanthemum	.	.	.	.	1	2	.	3	.	.	.	.	3	4	9	16
Poa pratensis	.	.	.	.	1	.	.	1	.	.	.	.	1	5	8	14
Agrimonia eupatoria	.	.	.	.	.	1	1	2	.	.	.	.	.	8	3	11
Mosses																
Pseudoscleropodium purum	.	.	.	8	19	14	1	42	.	.	.	3	33	12	2	50
Acrocladium cuspidatum	.	.	.	1	2	2	.	5	.	.	.	.	7	12	3	22
Eurhynchium praelongum	.	.	.	.	1	3	1	5	.	.	.	.	6	11	2	19
Brachythecium rutabulum	.	.	.	.	1	7	3	11	.	.	.	1	2	7	5	15
Mnium rostratum	.	.	.	1	.	5	.	6	.	.	.	1	3	6	3	13
" undulatum	.	.	.	.	.	12	.	3	.	.	.	.	2	7	2	12

(contd.)

Table 3 (contd.)

b) species with generally greater levels of abundance on the Oolite:

Abundance classes:	d	cd	va	a	f	o	r	Total	d	cd	va	a	f	o	r	Total
Zerna erecta	1	.	1	1	2	2	1	8	1	8	27	11	1	.	2	50
Cirsium acaule	.	.	.	3	19	12	4	38	.	.	9	9	21	6	4	49
Dactylis glomerata	.	.	.	1	3	7	5	16	.	.	.	4	21	9	12	46
Trifolium pratense	.	.	.	3	4	9	1	17	.	.	.	14	18	9	2	43
Leontodon hispidus	.	.	1	3	5	2	11	22	.	.	1	19	8	6	8	42
Brachypodium pinnatum	.	.	1	.	.	1	.	2	3	5	18	.	5	5	2	38
Medicago lupulina	.	.	.	.	3	6	3	12	.	.	.	11	20	5	1	37
Primula veris	.	.	.	.	.	2	2	4	.	.	.	.	12	14	10	36
Achillea millefolium	.	.	.	.	.	6	4	10	.	.	.	2	5	14	8	29
Knautia arvensis	.	.	.	.	.	1	.	1	.	.	.	.	8	14	6	28
Veronica chamaedrys	.	.	.	.	.	3	4	7	.	.	.	.	8	8	12	28
Bellis perennis	.	.	.	3	4	5	3	15	.	.	.	3	10	9	2	24
Centaurea nigra	.	.	.	.	.	2	4	6	.	.	.	.	8	5	10	23
Trisetum flavescens	.	.	.	.	.	.	5	5	.	.	.	.	3	6	13	22
Lathyrus pratensis	.	.	.	.	.	1	1	2	.	.	.	.	11	5	4	20
Centaurea scabiosa	.	.	.	.	.	.	1	1	.	.	.	.	3	7	8	18
Leontodon autumnalis	.	.	.	.	1	5	3	9	.	.	.	1	3	9	3	16
Crepis capillaris	.	.	.	1	.	.	6	7	.	.	.	.	1	4	10	15
Succisa pratensis	.	.	.	.	1	3	.	4	.	.	.	1	7	4	1	13
Thymus pulegioides	.	.	.	.	.	.	1	1	.	.	.	6	2	2	1	11
Trifolium medium	.	.	.	.	.	1	.	1	.	.	1	.	4	2	2	9
Hippocrepis comosa	.	.	.	.	.	1	.	1	.	.	.	2	2	1	3	8
Serratula tinctoria	.	.	.	.	.	.	1	1	.	.	1	1	1	.	3	6
Origanum vulgare	.	.	.	.	.	1	.	1	.	.	.	1	1	3	.	5

(contd.)

Table 3b (contd.)

Abundance classes:	d	cd	va	a	f	o	r	Total	d	cd	va	a	f	o	r	Total
Mosses																
Hypnum molluscum	.	.	.	.	4	6	1	11	.	.	.	2	15	11	1	29
Hylocomium squarrosum	.	.	.	2	1	7	1	11	.	.	.	3	6	8	2	19
Camptothecium lutescens		.	.	.	.	4	1	5	.	.	.	1	3	1	5	10
c) species with generally greater levels of abundance on the Carboniferous Limestone:																
Campanula rotundifolia		.	.	1	11	3	3	18	.	.	.	.	7	16	7	30
Helictotrichon pubescens		.	.	1	6	3	5	15	.	.	.	2	4	10	13	29
Anthyllis vulneraria		.	1	.	1	.	.	2	.	.	.	1	4	2	3	10

TABLE 4

Species with essentially similar frequency of occurrence on the two limestones.

a) with similar levels of abundance on the two limestones:

	Carboniferous Limestone								Oolitic Limestone							
	Number of times recorded as:							Total occurrences	Number of times recorded as:							Total occurrences
Abundance classes:	d	cd	va	a	f	o	r		d	cd	va	a	f	o	r	
Lotus corniculatus	.	.	.	32	12	3	2	49	.	.	.	37	12	1	.	50
Carex flacca	.	.	3	19	19	7	.	48	.	.	4	26	17	2	.	49
Briza media	.	.	2	12	20	11	.	45	.	.	1	14	25	4	2	46
Galium verum	.	.	.	7	18	18	2	45	.	.	.	2	29	10	3	44
Hieracium pilosella	.	.	.	23	18	7	.	48	.	.	2	18	14	8	2	44
Linum catharticum	.	.	.	3	29	8	2	42	.	.	.	5	31	11	.	47
Prunella vulgaris	.	.	.	4	24	10	.	38	.	.	.	1	29	10	.	40
Taraxacum officinale	.	.	.	1	12	19	4	36	.	.	.	.	10	12	10	32
Viola hirta	.	.	.	3	16	7	3	29	.	.	.	3	18	8	1	30
Helianthemum chamaecistus		1	4	11	7	2	1	26	.	.	8	10	4	2	3	27
Festuca rubra	.	.	1	10	9	6	1	27	.	.	1	9	4	8	.	22
Scabiosa columbaria	.	.	1	1	8	7	7	24	.	.	.	2	12	13	3	30
Holcus lanatus	.	.	.	3	1	4	5	13	.	.	.	2	6	3	4	15
Galium mollugo	.	.	.	.	.	4	8	12	.	.	.	.	1	6	5	12
Gentianella amarella	.	.	.	.	2	5	4	11	.	.	.	.	1	7	5	13
Luzula campestris	.	.	.	.	4	8	1	13	.	.	.	.	2	6	1	9
Quercus robur	.	.	.	.	.	3	6	9	.	.	.	.	1	5	5	11
Hypericum perforatum	.	.	.	.	3	2	4	9	.	.	.	.	1	.	2	3
Asperula cynanchica	.	.	.	.	2	1	4	7	.	.	.	.	2	1	3	6

(contd.)

Table 4a (contd.)

Abundance classes:	d	cd	va	a	f	o	r	Total	d	cd	va	a	f	o	r	Total
Trifolium campestre	.	.	.	.	1	1	3	5	.	.	.	.	.	3	6	9
Orchis fuchsii	.	.	.	.	.	3	1	4	.	.	.	.	1	1	5	7
Stachys officinalis	.	.	.	1	2	1	1	5	.	.	.	.	1	4	.	5
Fraxinus excelsior	.	.	.	.	.	.	3	3	.	.	.	.	.	2	3	5
Sonchus asper	.	.	.	.	.	.	3	3	.	.	.	.	.	.	4	4
Inula conyza	.	.	.	.	.	1	2	3	.	.	.	1	.	1	1	3
Ajuga reptans	.	.	.	.	.	1	.	1	.	.	.	.	.	1	.	1
Arenaria serpyllifolia.	.	.	.	.	.	.	3	3	.	.	.	.	.	.	1	1
Arrhenatherum elatius	.	.	.	.	.	1	2	3	.	.	.	.	.	1	1	2
Clinopodium vulgare	.	.	.	.	.	1	1	2	.	.	.	.	.	1	2	3
Daucus carota	.	.	.	1	2	.	.	3	.	.	.	.	.	.	2	2
Desmazeria rigida	.	.	.	.	.	.	1	1	.	.	.	.	.	.	1	1
Festuca arundinacea	.	.	.	.	.	.	1	1	.	.	.	.	.	1	.	1
Glechoma hederacea	.	.	.	.	.	1	1	2	.	.	.	.	.	2	1	3
Rhinanthus major	.	.	.	.	.	1	.	1	.	.	.	.	.	1	.	1
Rosa canina	.	.	.	.	.	.	1	1	.	.	.	.	.	.	1	1
Sherardia arvensis	.	.	.	.	.	1	.	1	.	.	.	.	.	1	1	2
Tragopogon pratense	.	.	.	.	.	.	2	2	.	.	.	.	.	.	1	1
Bryophytes.																
Barbula unguiculata	.	.	.	.	3	5	8	16	.	.	.	.	5	8	4	17
Hylocomium splendens	.	.	1	.	3	5	1	10	.	.	.	.	4	3	.	7
Thuidium tamariscinum	.	.	.	1	2	6	.	9	.	.	.	3	2	5	1	11
Mnium cuspidatum	.	.	.	.	.	2	3	5	.	.	.	.	.	1	2	3
Lophocolea bidentata	.	.	.	.	1	3	.	4	.	.	.	.	1	4	1	6
Plagiochila asplenioides	.	.	.	.	2	4	.	6	.	.	.	.	1	2	.	3

(contd.)

Table 4 (contd.)

b) with greater levels of abundance on the Carboniferous Limestone:

Abundance classes:	d	cd	va	a	f	o	r	Total	d	cd	va	a	f	o	r	Total
Festuca ovina	.	17	21	5	6	1	.	50	.	1	16	16	9	5	.	47
Poterium sanguisorba	.	.	16	23	5	.	3	47	.	1	6	30	9	1	3	50
Plantago lanceolata	.	.	3	17	10	12	2	44	.	.	.	9	28	5	1	43
Potentilla reptans	.	.	.	1	.	3	1	5	.	.	.	.	.	.	6	6
c) with greater levels of abundance on the Oolite																
Ranunculus bulbosus	.	.	.	5	13	15	7	40	.	.	.	11	18	8	9	46
" acris	.	.	.	.	.	1	3	4	.	.	.	.	2	3	.	5
Mosses.																
Fissidens taxifolius	.	.	.	.	5	12	11	28	.	.	.	2	19	12	1	34
Hylocomium triquetrum	.	.	.	1	4	4	2	11	.	.	.	5	3	2	4	14

TABLE 5

Species found only on the Carboniferous Limestone:

	Carboniferous Limestone								Oolitic Limestone							
	Number of times recorded as:							Total occurrences	Number of times recorded as:							Total occurrences
Abundance classes:	d	cd	va	a	f	o	r		d	cd	va	a	f	o	r	
Viola reichenbachiana	.	.	.	2	6	5	.	13	.	.	.	.	.	.	.	.
Erica cinerea	.	.	.	.	4	1	4	9	.	.	.	.	.	.	.	.
Calluna vulgaris	.	.	1	2	1	1	3	8	.	.	.	.	.	.	.	.
Aira caryophyllea	.	.	.	.	1	2	4	7	.	.	.	.	.	.	.	.
Rubus, Subgenus: Rubus.	.	.	.	.	.	1	6	7	.	.	.	.	.	.	.	.
Agrostis canina	.	.	1	.	1	2	.	4	.	.	.	.	.	.	.	.
Carex pulicaris	.	.	.	1	.	1	1	3	.	.	.	.	.	.	.	.
Plantago coronopus	.	.	.	1	1	.	1	3	.	.	.	.	.	.	.	.
Pteridium aquilinum	.	.	.	1	.	2	.	3	.	.	.	.	.	.	.	.
Viburnum opulus	.	.	.	.	.	.	2	2	.	.	.	.	.	.	.	.
Acer pseudoplatanus	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.
Anemone nemorosa	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.
Carduus nutans	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.
Carex humilis	.	1	.	.	.	.	.	1	.	.	.	.	.	.	.	.
Castanea sativa	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.
Erodium cicutarium	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.
Helianthemum appentrinum	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.
Koeleria vallesiana	.	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.
Lathyrus montanus	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.
Ligustrum vulgare	.	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.

(contd.)

Table 5: (contd.)

Abundance classes:	d	cd	va	a	f	o	r	Total	d	cd	va	a	f	o	r	Total
Mentha arvensis	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.
Quercus ilex	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.
Sedum acre	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.
Ulex gallii	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.
Vaccinium myrtillus	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.
Bryophytes and Lichens.																
Bryum obconicum	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.
Camptothecium sericeum	.	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.
Fissidens bryoides	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.
Neckera crispa	.	.	.	.	.	.	2	2	.	.	.	.	.	.	.	.
Polytrichum juniperinum	.	.	.	.	.	1	1	2	.	.	.	.	.	.	.	.
Trichostomum tortuosum	.	.	.	.	.	2	.	2	.	.	.	.	.	.	.	.
Frullania tamarisci	.	.	.	4	1	2	1	8	.	.	.	.	.	.	.	.
Lophozia attenuata	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.
Madotheca platyphylla	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.
Peltigera canina	.	.	.	.	.	2	4	6	.	.	.	.	.	.	.	.

TABLE 6

Species found only on the Oolite.

	Carboniferous Limestone								Oolitic Limestone							
	Number of times recorded as:							Total occurrences	Number of times recorded as:							Total occurrences
Abundance classes:	d	cd	va	a	f	o	r		d	cd	va	a	f	o	r	
Ononis repens	.	.	.	.	.	.	.	.	.	.	.	1	5	13	4	23
Campanula glomerata	.	.	.	.	.	.	.	.	.	.	.	1	4	3	5	13
Vicia cracca	.	.	.	.	.	.	.	.	.	.	.	.	5	1	2	8
Agrostis stolonifera	.	.	.	.	.	.	.	.	.	.	.	.	1	2	4	7
Picris hieracioides	.	.	.	.	.	.	.	.	.	.	.	.	1	1	5	7
Genista tinctoria	.	.	.	.	.	.	.	.	.	.	.	1	1	2	2	6
Convolvulus arvensis	.	.	.	.	.	.	.	.	.	.	.	.	.	2	3	5
Rumex acetosa	.	.	.	.	.	.	.	.	.	.	.	.	1	.	4	5
Alopecurus pratensis	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	4
Cirsium arvense	.	.	.	.	.	.	.	.	.	.	.	.	.	1	3	4
Onobrychis viciifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	1	3	4
Polygala calcarea	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2	4
Corylus avellana	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	3
Thesium humifusum	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	3
Valeriana officinalis	.	.	.	.	.	.	.	.	.	.	.	.	1	.	2	3
Heracleum sphondylium	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2
Lolium perenne	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	2
Orchis mascula	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2
Conopodium majus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1

(contd.)

Table 6 (contd.)

Abundance classes:	d	cd	va	a	f	o	r	Total	d	cd	va	a	f	o	r	Total
Echium vulgare	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
Erigeron acris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
Fagus sylvatica	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
Galium cruciata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
Geranium columbinum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
Myosotis arvensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
Pastinaca sativa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
Plantago major	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1
Ranunculus repens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
Tetragonolobus siliquosus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
Bryophytes and lichens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Bryum capillare	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
Neckera complanata	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1
Trichostomum crispulum	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1
Aneura major	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
Cladonia fimbriata	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1

Discussion

Although the data in Tables 2-6 are based on subjective determinations and can show only the Fidelity of species (presence or absence on an area) and broad features of relative abundance, a number of points emerge from a comparison of the two grassland-types in this manner.

Few species (Tables 5 and 6) were found to be exclusive to either grassland-type; moreover it was unusual for any of these to occupy an important part of the vegetation-cover. Thus on Carboniferous Limestone (Table 5) Agrostis canina and Calluna vulgaris were 'va', and Carex humilis 'od' on only a single occasion for each species, and a number of others rarely had estimates of 'abundant', e.g. Viola reichenbachiana. On the Oolite, (Table 6) the only exclusive species to reach 'abundant' were Genista tinctoria (once) and Campanula glomerata (once).

Therefore, taking the 100 areas as a whole, the variety of species in the vegetation-cover is very similar on the two limestones. However, the frequency of

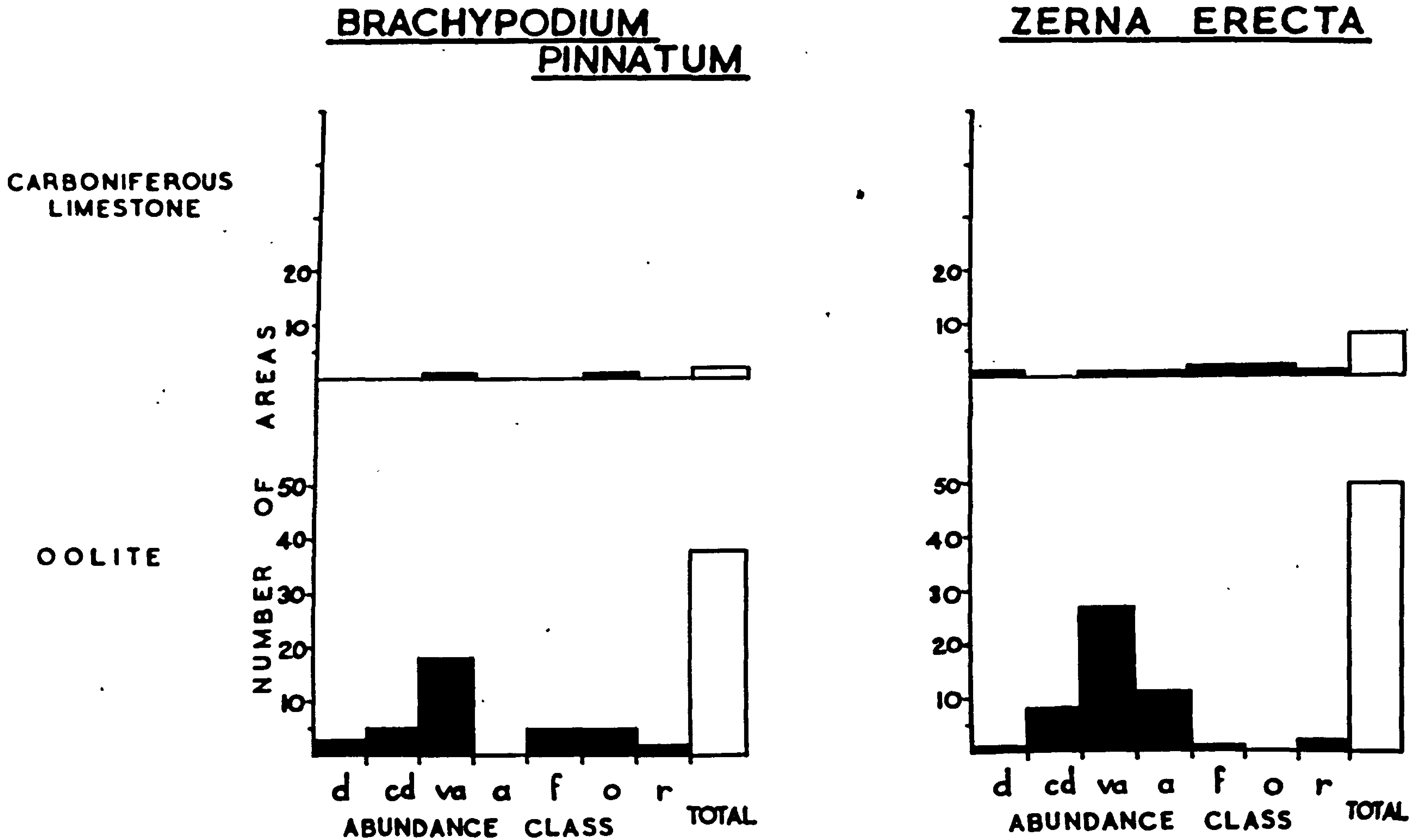


Figure 4. Comparison of the behaviour of B.pinnatum and Z. erecta in calcareous grassland on the two limestones.

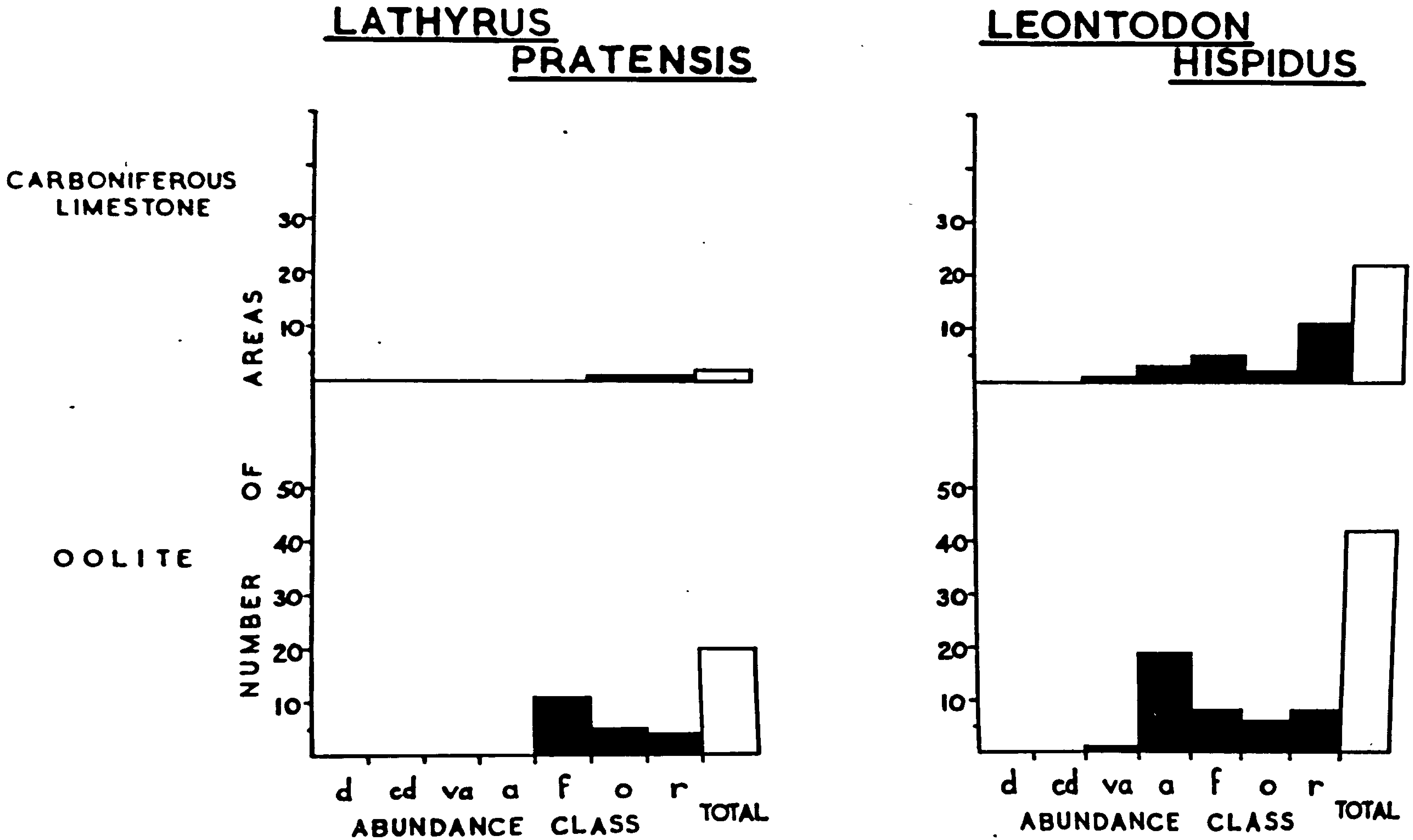
occurrence and relative abundance in the turf of many of the constituent species differ markedly in the two types (Tables, 2,3,4b,4c).

During the following discussion of the various species-groups, reference to frequency - histograms of individual examples (Figs. 4-11) will facilitate comparison for the two limestones.

Several general trends in the floristic composition of the two types of grassland may be recognized:-

1. <u>The differential occurrence of tall and short species on the two limestones.</u>

As was indicated in the description of physiognomy (page 19.), the most obvious difference between the two grasslands is in the occurrence of the tall-growing grasses, <u>Zerna erecta</u> and <u>Brachypodium pinnatum</u>. <u>Zerna erecta</u> is universally present on the Oolitic limestone, generally at high levels of abundance, and is frequently (38 out of 50 areas) in association with <u>Brachypodium pinnatum</u>, itself usually 'va' or above (cf. Fig. 4). These two species are of very limited occurrence on the Carboniferous Limestone; only once (at Draycott, cf. physiognomy, p. 20.) were they found growing in close association, together



LATHYRUS PRATENSIS
LEONTODON HISPIDUS
CARBONIFEROUS LIMESTONE
OOLITE
NUMBER OF AREAS
10
20
30
40
50
d cd va a f o r TOTAL
ABUNDANCE CLASS

Figure 5.

dominating the herbage in a manner characteristic of the Oolite.

The widespread preponderance of these taller grasses on the Oolite produces a very different environment for subsidiary species than that obtaining in the low-growing Fescue - herb communities, common on the Carboniferous Limestone. This difference in micro-environment over the two limestones is probably responsible for differences in the behaviour of a number of subsidiary species. Thus it may be observed that a large number of the species more characteristic of the Oolite (Tables 3,6) are of tall or robust habit. The important species of this type are listed in Table 7. (cf. Fig.5).

TABLE 7

Achillea millefolium	Medicago lupulina
Centaurea nigra	Ononis repens
" scabiosa	Serratula tinctoria
Dactylis glomerata	Thymus pulegioides
Lathyrus pratensis	Trifolium pratense
Leontodon hispidus	

The greater frequency of occurrence and/or greater abundance of the following mosses on the Oolite (Tables 3a,3b; cf. Fig.6)

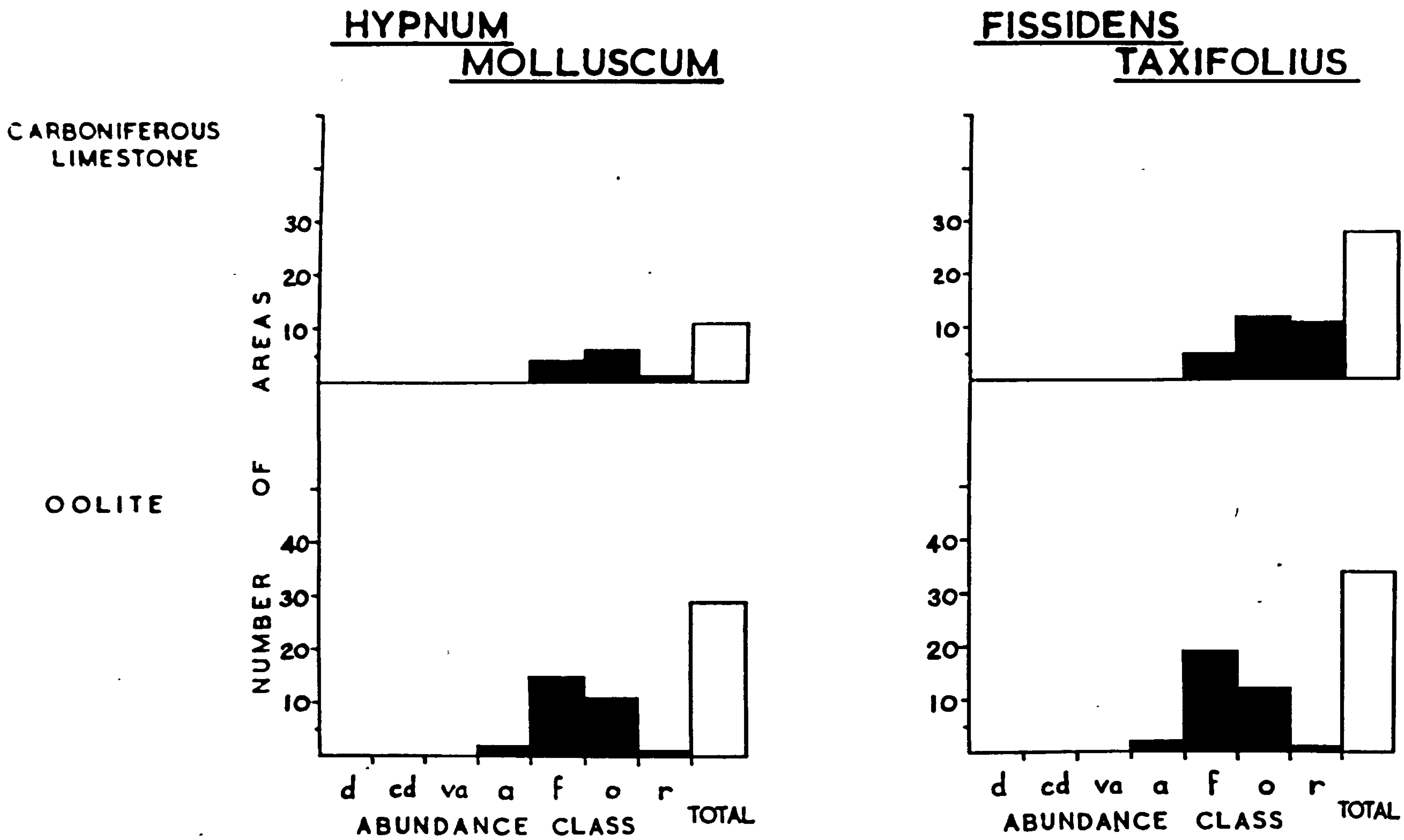

HYPNUM MOLLUSCUM
FISSIDENS TAXIFOLIUS
CARBONIFEROUS LIMESTONE
OOLITE
NUMBER OF AREAS
10
20
30
40
d cd va a f o r TOTAL
ABUNDANCE CLASS

Figure 6.

may be associated with the generally taller vegetation:

Acrocladium cuspidatum	Hylocomium triquetrum
Brachythecium rutabulum	Hypnum molluscum
Eurhynchium praelongum	Minum rostratum
Fissidens taxifolius	" undulatum;
Hylocomium squarrosum	Pseudoscleropodium purum;

on both limestones, these mosses were conspicuous only on areas with tall vegetation.

On the other hand, most of the species with more frequent occurrence and/or greater abundance on the Carboniferous Limestone (Tables 2,4b; cf. Fig.7) are of low-growing habit or rosette-form. Species of this type are listed in Table 8.

TABLE 8.

Agrostis tenuis	Koeleria gracilis
Carex caryophyllea	Leontodon leysseri
Carlina vulgaris	Plantago lanceolata
Centaurium minus	Poterium sanguisorba
Euphrasia nemorosa	Senecio jacobaea
Festuca ovina	Spiranthes spiralis
Helictotrichon pratense	Thymus drucei
Hypochaeris radicata	

The mosses Dicranum scoparium and Hypnum cupressiforme, and the lichens Cladonia rangiformis and C. furcata, more frequently occurring on the Carboniferous Limestone, were

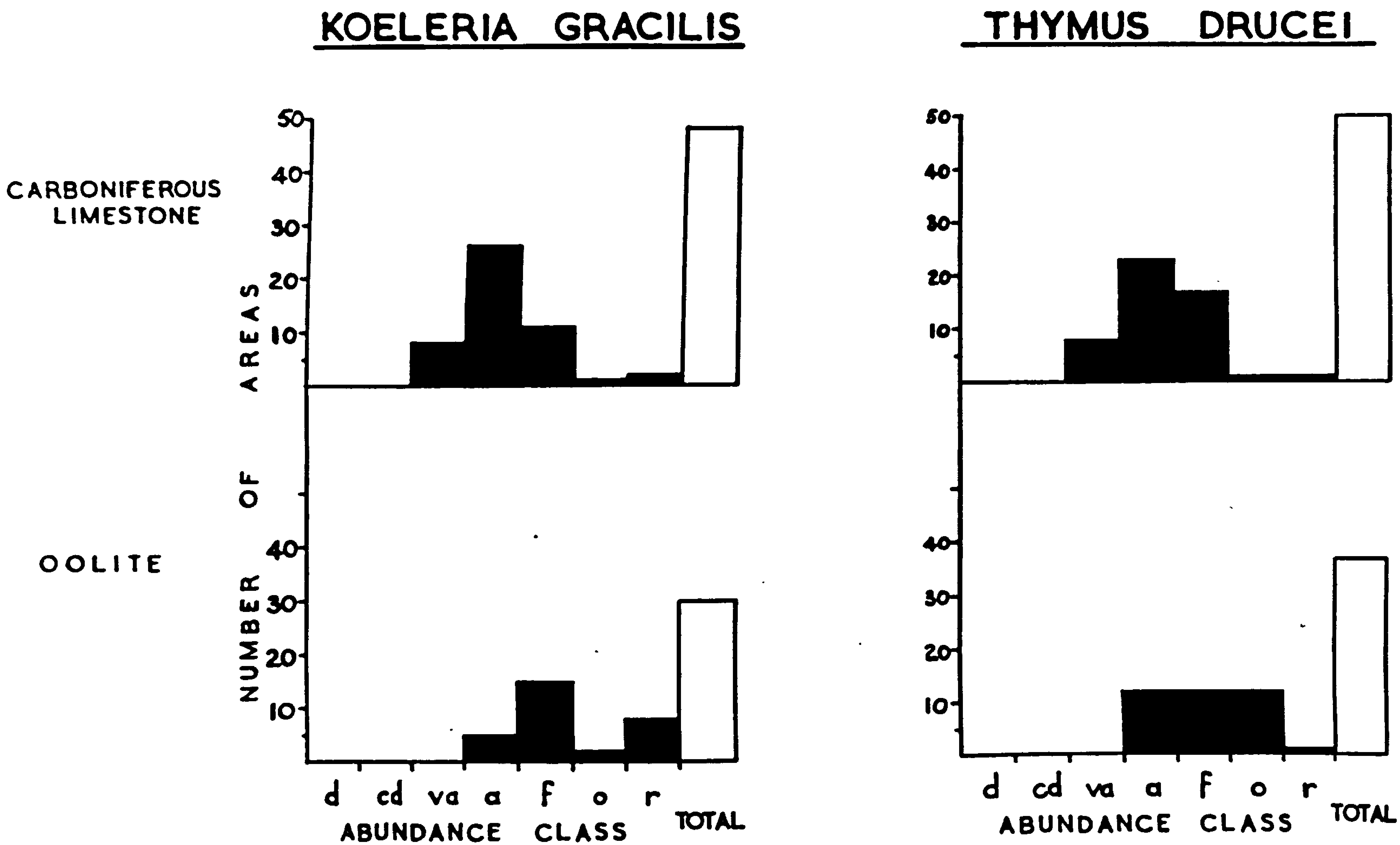

KOELERIA GRACILIS
THYMUS DRUCEI
CARBONIFEROUS LIMESTONE
OOLITE
NUMBER OF AREAS
50
40
30
20
10
d cd va a f o r TOTAL
ABUNDANCE CLASS

Figure 7.

present on both limestones only on areas with low average heights of herbage.

Apart from a general correlation of differences in behaviour of species with differences in average height of the herbage over the two limestones (cf. Fig.2,p.21), evidence for classifying the species in Tables 7 and 8 has been provided on many individual areas on both limestones. For example, the five areas on the Oolite showing Koeleria 'abundant' were all well-grazed, with low herbage (average heights: 6,6,6,4,3 cm. respectively). On Carboniferous Limestone, the three areas showing Koeleria 'rare' or 'occasional' were ungrazed, with tall herbage (average heights: 13,10,15 cm. respectively). Thus it seems probable that a moderately high abundance of Koeleria is correlated with a short height of herbage.

2. The more frequent occurrence of 'acidic' species on the Carboniferous Limestone.

A hardly less striking floristic difference between the two grasslands is the frequent, almost general occurrence on the Carboniferous Limestone of species often present on acid soils, and the very scattered occurrence

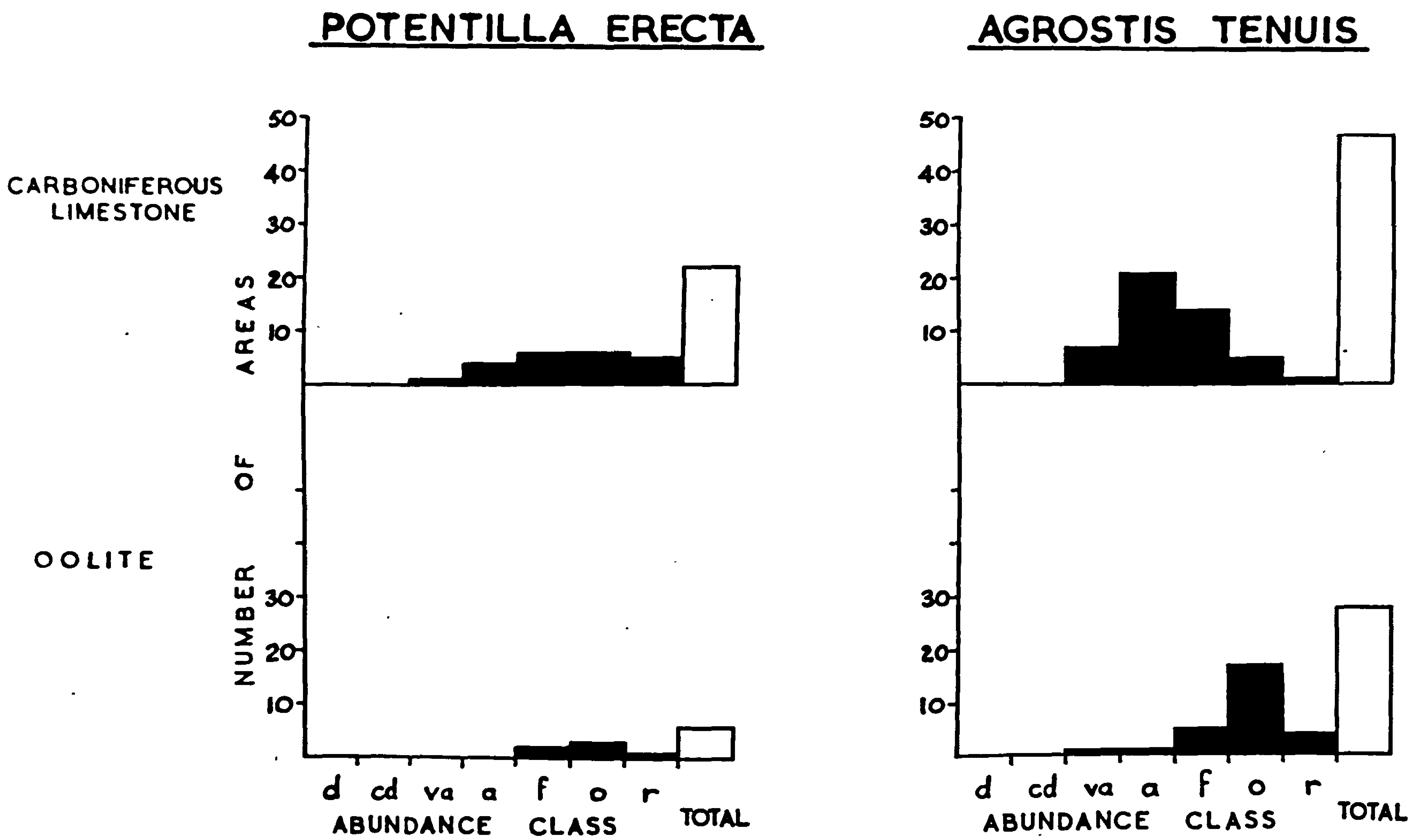

POTENTILLA ERECTA
AGROSTIS TENUIS
CARBONIFEROUS LIMESTONE
OOLITE
NUMBER OF AREAS
50
40
30
20
10
d cd va a f o r
ABUNDANCE CLASS
TOTAL

Figure 8.

of these species on the Oolite (Table 2; cf. Fig.8.) Species in this category are listed in Table 9. Some species from Table 5 which are characteristic of acid soils are also included; these were exclusive to the Carboniferous Limestone, though of infrequent occurrence. Agrostis tenuis shows moderately high frequencies of occurrence on the Oolite but generally at lower levels of abundance than on the Carboniferous Limestone (Fig.8).

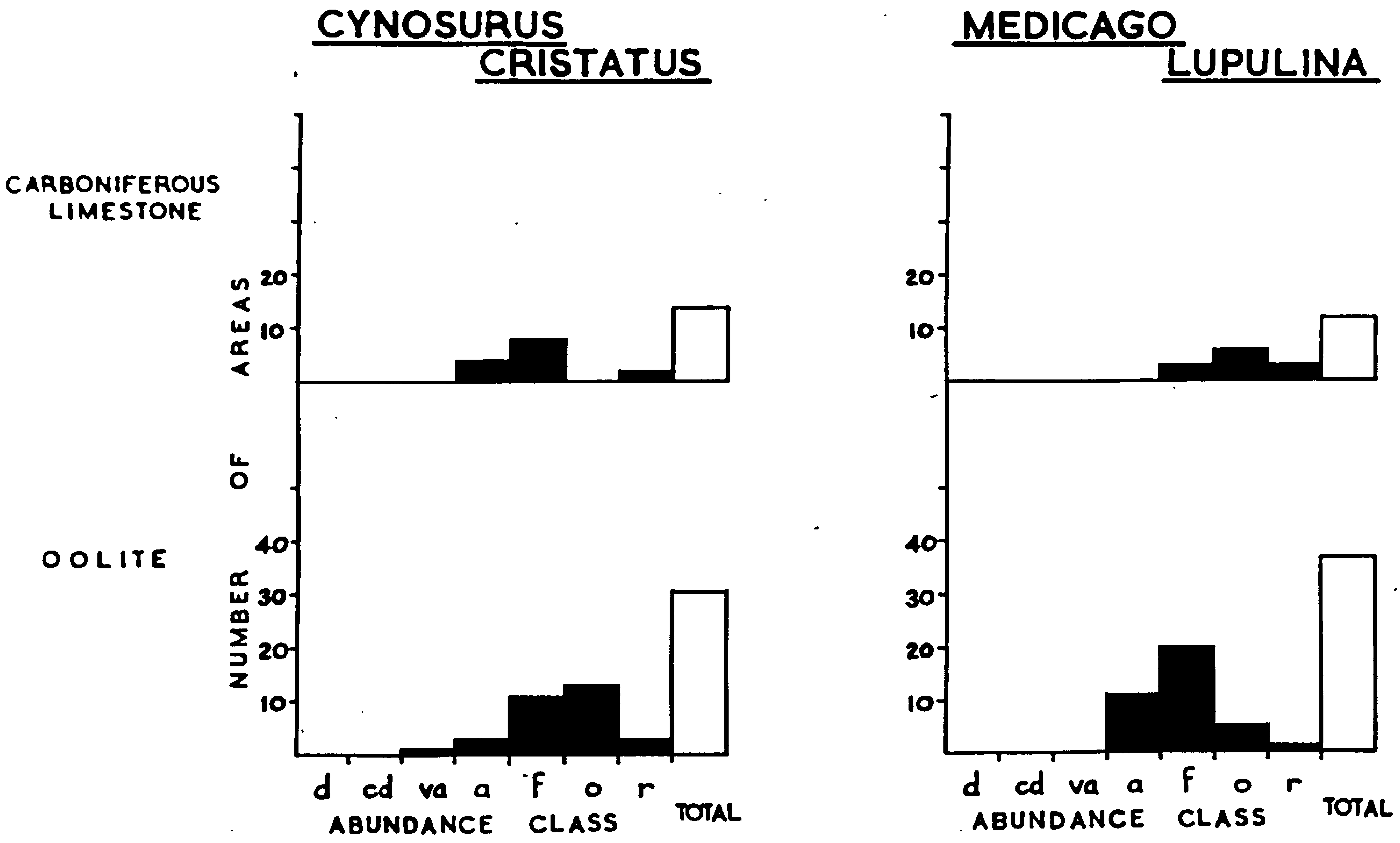
TABLE 9.

Agrostis tenuis	Veronica officinalis
Potentilla erecta	Viola riviniana
Sieglingia decumbens	

Species exclusive to Carboniferous Limestone:

Agrostis canina	Ulex gallii
Calluna vulgaris	Vaccinium myrtillus
Erica cinerea	Viola reichenbachiana

Most of these species were observed to be regular members of heathland vegetation on acid soils of both the Mendips and the Cotswolds; yet only in a few areas, mostly in steep and rocky situations with very shallow soil, were species of this type entirely lacking in calcareous grassland on the Carboniferous Limestone, whereas on the Oolite areas, the occurrence of the more marked calcifuge species, such as Potentilla erecta or Veronica officinalis was very rare indeed. An admixture of heathland species has been widely



CYNOSURUS CRISTATUS
MEDICAGO LUPULINA
CARBONIFEROUS LIMESTONE
OOLITE
NUMBER OF AREAS
10
20
30
40
d
cd
va
a
f
o
r
TOTAL
ABUNDANCE CLASS

Figure 9.

observed in the calcareous grasslands of the Carboniferous Limestone (e.g. Moss, 1913, Balme, 1953), and it appears to be characteristic of this rock-formation.

3. The more frequent occurrence of 'agricultural' species on the Oolitic limestone.

A large number of species with higher frequencies of occurrence and/or greater levels of abundance on the Oolitic limestone (Tables 3,4c; cf. Fig.9), although common members of the semi-natural calcareous grassland of both limestones, are plants seen in particular abundance in places very strongly affected by agricultural operations e.g. in arable fields, on land especially heavily grazed by farm-animals, on farm tracks or in gateways. These are listed in Table 10.

TABLE 10.

Achillea millefolium	Leontodon autumnalis
Agrimonia eupatoria	" hispidus
Bellis perennis	Medicago lupulina
Centaurea nigra	Plantago media
" scabiosa	Primula veris
Chrysanthemum leucanthemum	Trifolium pratense
Crepis capillaris	" repens
Cynosurus cristatus	Ranunculus acris
Dactylis glomerata	" bulbosus
Knautia arvensis	Veronica chamaedrys

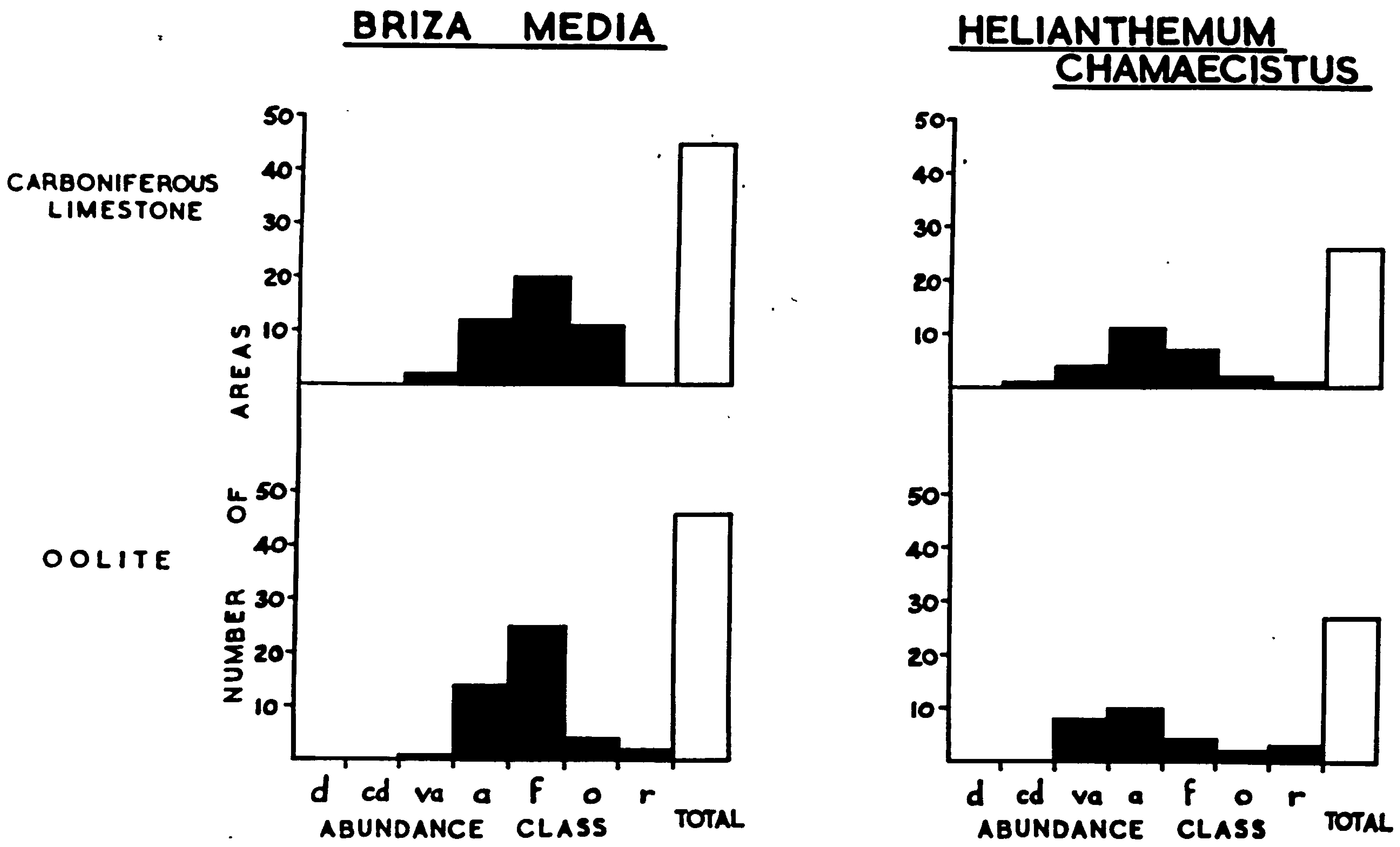

BRIZA MEDIA
HELIANTHEMUM CHAMAECISTUS
CARBONIFEROUS LIMESTONE
OOLITE
NUMBER OF AREAS
50
40
30
20
10
d cd va a f o r
TOTAL
ABUNDANCE CLASS

Figure 10.

Species falling into this category, but with similar frequencies of occurrence on the two limestones are:

Holcus lanatus	Prunella vulgaris
Plantago lanceolata	Taraxacum officinale.

4. <u>The similar behaviour of a number of species on two limestones.</u>

There is a group of species (Table 4a; cf. Fig.10) which occur with roughly equal frequencies and at similar levels of abundance on the two limestones. Species in the higher grades of total frequency of occurrence e.g. <u>Briza media</u>, <u>Carex flacca</u>, must be regarded as equally tolerant of the range of environmental conditions on each limestone. Excluding casuals, the species with lower frequencies, e.g. <u>Helianthemum chamaecistus</u>, <u>Festuca rubra</u> may be regarded in the same way, although the factors resulting in a similar behaviour may be different for the two limestones. For example <u>Helianthemum</u> is generally absent or present in low abundance on areas with a conspicuous abundance calcifuge flora on Carboniferous Limestone; and it does not occur extensively in many of the tallest <u>Zerna</u> - <u>Brachypodium</u> communities on the Oolite. Thus the presence of <u>Helianthemum</u> may be limited by tall herbage

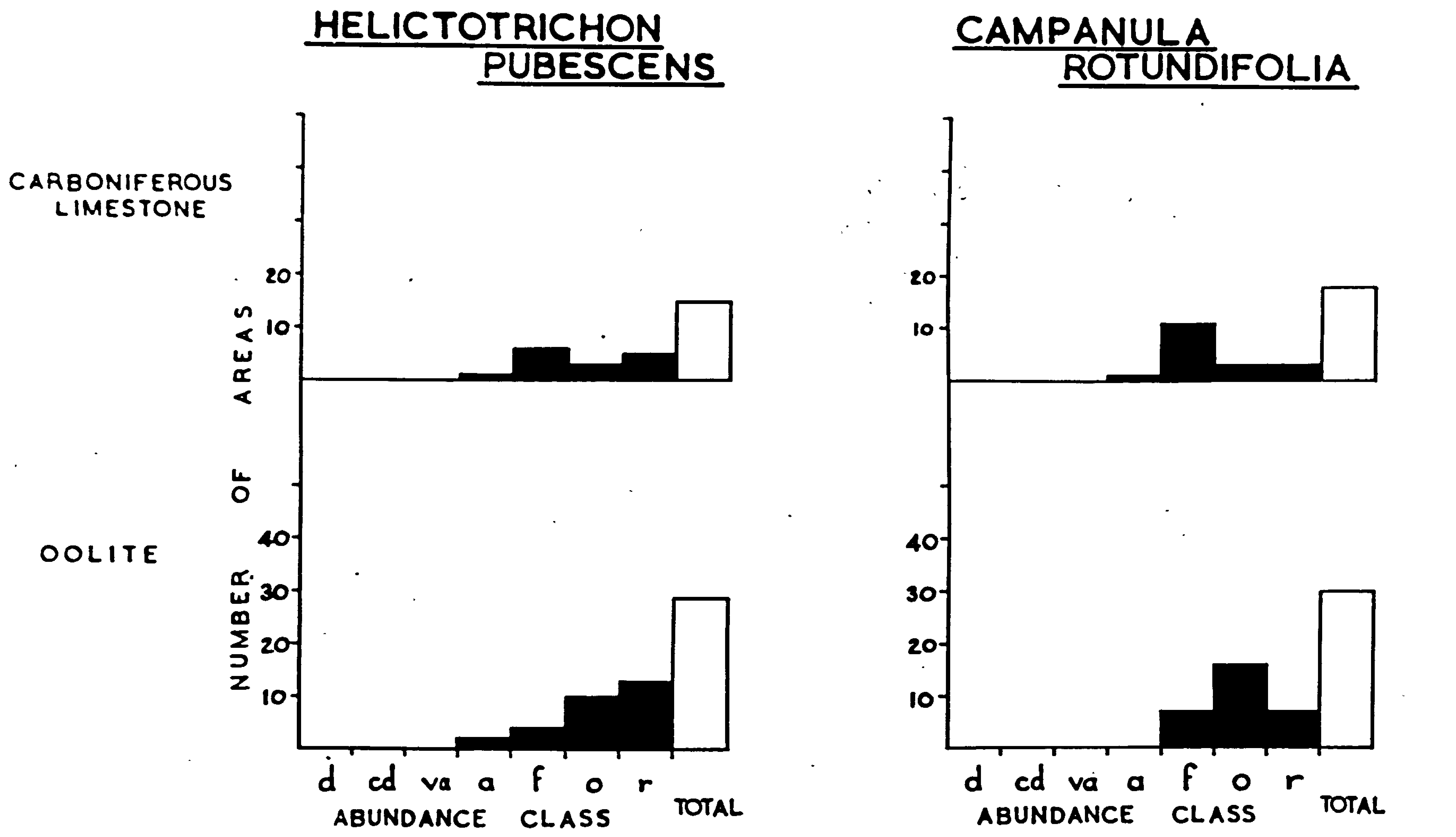

HELICTOTRICHON PUBESCENS
CAMPANULA ROTUNDIFOLIA
CARBONIFEROUS LIMESTONE
OOLITE
NUMBER OF AREAS
10
20
30
40
d cd va a f o r
TOTAL
ABUNDANCE CLASS

Figure 11.

on the Oolite, but by other factors on the Carboniferous Limestone.

5. Species occurring more frequently on one limestone but in greater abundance on the other.

The Two species in Table 3c, Heliototrichon pubescens and Campanula rotundifolia show a peculiar type of behaviour (cf. Fig.11): both are present on a larger number of areas on the Oolite, yet at lower levels of abundance than when occurring on the Carboniferous Limestone.

Anthyllis vulneraria may also be included in this category, though it occurs infrequently on both limestones.

6. Species that cannot be placed in any of the five categories above.

Leaving aside casual species of similar frequencies of occurrence (in Table 4b) there are a few species (Table 11) which do not fit readily into the broad categories of Tables 7-10 apparent from general field-observation.

TABLE 11

Blackstonia perfoliata	Pimpinella saxifraga
Brachypodium sylvaticum	Polygala vulgaris
Crataegus monogyna	Succisa pratensis
Cirsium acaule	Teucrium scorodonia
" palustre	Trisetum flavescens
Filipendula vulgaris	
Fragaria vesca	Camptothecium lutescens
Origanum vulgare	Frullania tamarisci
Phleum nodosum	

The following observations may help towards an understanding of the factors responsible for a differential behaviour of some of these species: The more frequent occurrence of Filipendula vulgaris and Cirsium palustre on the Carboniferous Limestone may be related to a leached surface soil common on this rock-formation, although it is known that these species are by no means calcifuge. Five of the eleven Oolite records of Filipendula were on areas showing Potentilla erecta. Cirsium palustre occurred on the acid soil of the Harford Sands, Cleeve Hill, but it was absent from the adjacent Oolitic calcareous grassland. Blackstonia perfoliata, more frequent on the Oolite, may be associated with an open turf, which is of general occurrence on this limestone. 6 of the 8 areas with Blackstonia on the Carboniferous Limestone are in situations with conspicuously open turf, while many of the

Oolite records are from very open turf. The presence of Cirsium acaule may also be influenced by the closeness of the turf: a number of areas on the Oolite with a more crowded vegetation-cover than is usual on this limestone showed C. acaule 'rare' or 'occasional'. Thus the generally close turf may reduce the abundance of this plant on the Carboniferous Limestone. All areas showing Frullania tamarisci on Carboniferous Limestone were fully exposed to wind-action and carried a very short herbage, conditions rarely experienced on the Oolite.

Summary.

While the majority of species recorded are common to both types of grassland, and some of these show similar behaviour on the two limestones, very marked and widespread differences in floristic composition were observed.

Calcareous grassland on Oolitic limestone characteristically contains Zerna erecta, often in great abundance, and generally in association with quantities of Brachypodium pinnatum, producing a moderately tall, coarse and open herbage. There is an abundance of

associated herbs, with taller species preponderating, and with a conspicuous occurrence of 'agricultural' species; species characteristic of acid soils are of very rare occurrence.

On the Carboniferous Limestone, calcareous grassland is typically free of both *Z. erecta* and *B. pinnatum* and the turf is short and close, with Fescue and low-growing herbs preponderating. A number of species characteristic of acid soils are of very general occurrence and frequently form an important part of the herbage; agricultural species are not of conspicuous occurrence.

Phot. 9. Shute Shelve Hill, near Axbridge. Mendip escarpment in the background (right). Clumps of gorse in the middle of the slope; hawthorn and bracken below. Like most of the south face of the Mendips, this slope overlooks a large area of low-lying country (Somerset Levels), which extends to the coast.

Phot. 10. A west slope bearing calcareous grassland on the Oolite, at West Yatton Down, near Castle Combe. As in many of the Oolite areas, this slope is well sheltered from the winds by the opposite sides of the valley.

IV. Investigation of environmental factors.

From general observation and field-experience on the two series of grasslands, the following features of the environment have been noted:

Aspect.

The aspects of the recorded areas are shown in the frequency-histograms of Fig.12. Though fewer areas faced north and rather more faced south on the Carboniferous Limestone, there is no very marked difference in the numbers of areas with the various aspects on the two limestones.

Degree of slope.

The numbers of areas with the different categories of steepness are essentially similar on the two limestones (cf. Fig.12), though a few more moderately steep areas were recorded from the Oolite.

Exposure to wind.

The Mendip Hills are conspicuously more exposed to the action of wind; this range of hills rises more prominently from the surrounding country and is nearer the sea than the Cotswold Hills. Moreover the main axis of

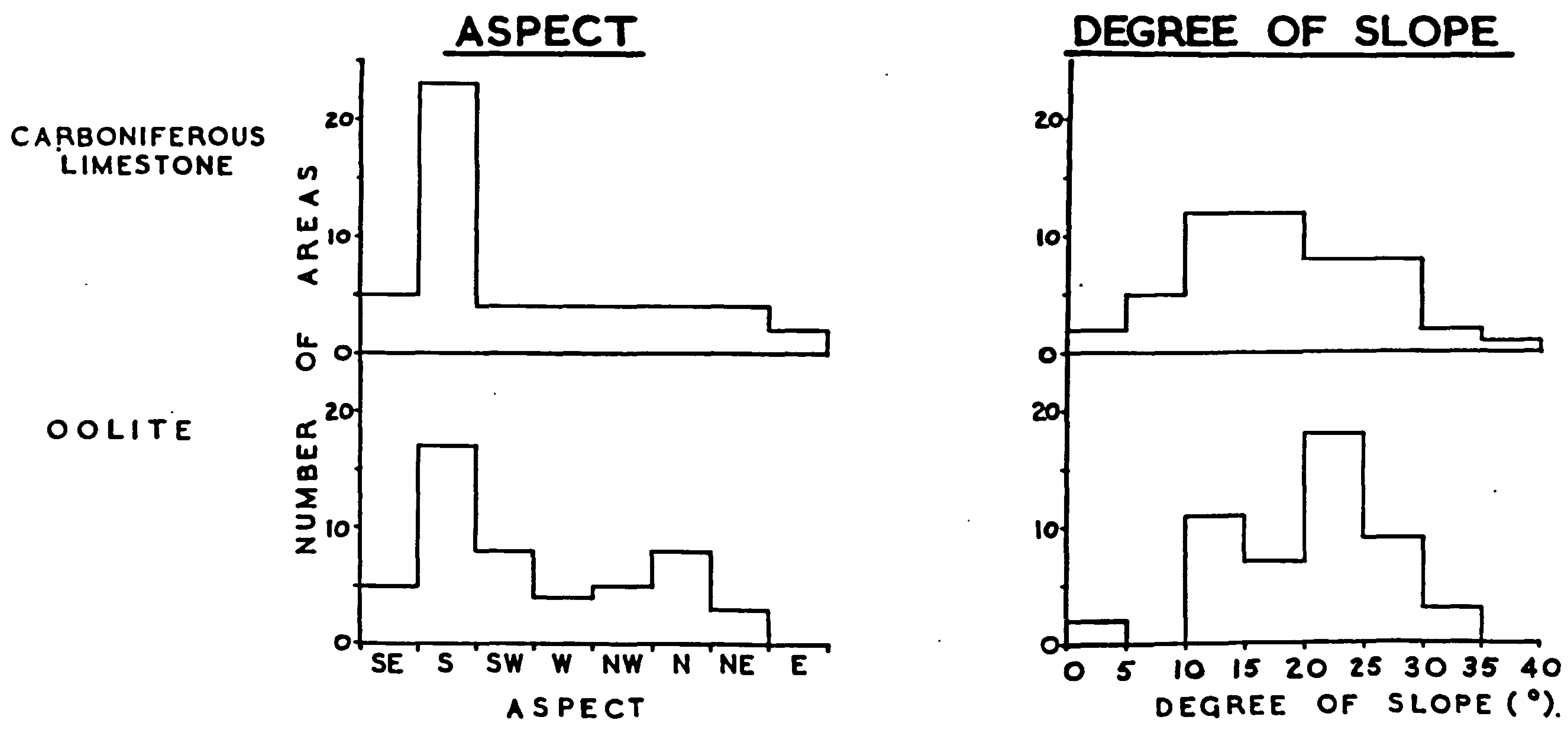


Figure 12. Comparison of aspect and degree of slope of the recorded areas on the two limestones.

the Mendip Hills lies at right angles to the path of the prevailing south-west winds whereas the line of the Cotswold Hills is roughly parallel to their direction. Thus the force of winds impacts more suddenly on the Carboniferous Limestone outcrop. It is mainly because of this, but also because of the sscarcity of trees and hedges on the Mendips, that individual areas of calcareous grassland on this hill-formation are very open to the influence of wind (cf. Table 12). While much of the Cotswold plateau is very windswept, the winds are less severe than on the Mendips. Furthermore, the effect of winds on the calcareous grasslands of the Cotswolds is much diminished, because most of these areas are on the sloping sides of valleys, more or less sheltered by hedges or trees.(cf.Phot.9,10 ;p.52).

TABLE 12

Summary of observations on the recorded areas regarding openness to wind action.

Exposure to wind	Number of areas	
	Carboniferous Limestone	Oolitic Limestone
Fully exposed	31	4
Partially sheltered by land-topography and/or trees and hedges.	8	13
Well sheltered	11	33

The climate of the Mendip Hills is typically upland in character (Moss, 1907) and the same is true for the higher points of the Cotswolds (Beckinsale, 1948). However the climate is less severe over much of the Cotswold country on the dipslopes east of the escarpment. The figures quoted by Moss, and Beckinsale show that much of the Mendips has a distinctly higher mean annual rainfall than the Cotswold Hills. Thus on the Mendips east of Cheddar, the mean annual rainfall is greater than 40 in., and, on some of the higher points, approaches 50 in. On the greater part of the Cotswold Hills the mean annual rainfall is 32-34 in., but reaches 38 in. on some of the higher ground near the escarpment.

Grazing.

Observations on present grazing intensities were very subjective and depended to a great extent on circumstantial evidence. From estimates of the intensity of grazing at the time of recording, areas have been classified into 4 grades (Table 13).

TABLE 13

Summary of the estimated intensities of grazing on the recorded areas.

Intensity of grazing	Number of areas	
	Carboniferous Limestone	Oolitic Limestone
Little grazed	12	9
Moderately grazed	15	16
Heavily grazed	19	21
Very heavily grazed	2	2

There appears to be practically no general difference in intensity of grazing on the calcareous grasslands of the two limestones at the present time. However there may be a difference in the type of grazing: it was observed that the Mendip grasslands supported fewer cattle, though rabbits may have been more abundant, than in the Cotswold area.

Referring to the accounts on the use of land on the Cotswolds (Price 1948) and on the Mendips (Moss 1907), there are indications of a difference in past-history of the grasslands of the two limestones. It seems that the Cotswold area has been more affected by the fluctuating agricultural policy of the last 150 years or so, because the land here is more amenable to intensive farming. Hence grazing by rabbits and perhaps sheep may have continued in a more regular way over larger areas of land on the Mendip Hills.

Investigation of edaphic conditions.

Edaphic conditions on the two limestones were investigated in two main ways:

1. In the field, by detailed descriptions of complete profiles on each limestone-formation, supplemented by data from the upper part of the soil profile on each recorded area.
2. In the laboratory, by detailed analyses of soil samples taken from a number of selected grassland areas.

1. <u>Descriptions of the soil profiles.</u>

Descriptions of complete profiles on both limestones were made from exposed faces of disused quarries in open grassland. For each description a uniform part of quarry face 3 or 4 feet wide was chosen, and a superficial layer of soil - and rock-material, approximately 6 in. thick, was removed from the exposed surface of the profile. Loose soil and stones were cleaned away to show up the structural features of the soil-profile <u>in situ</u>, and description then followed the recognized British method (Clarke, 1941).

<u>The Carboniferous Limestone profile</u>

Inspection of a number of complete profiles on the Carboniferous Limestone showed that these are of two main types, depending on the thickness of limestone fragments above the massive parent rock. In the first type the superficial stoneless soil passes almost immediately to the massive limestone beneath, with only a very thin layer of limestone fragments. The second type shows a considerable thickness of fragmented limestone above the parent rock.

Example of Type 1 profile (Surface soil passing abruptly to the massive parent rock). (Phot. 11a, p. 65).

Face of a quarry at Long Ashton; situated in nearly level ground.

Vegetation: open, ungrazed turf; mainly *Zerna erecta*, with *Festuca ovina* and a few dicotyledons.

Profile description

0-3 in.	Thin layer of vegetable debris and a very thin, nearly black surface layer of humus, overlying brownish dark red, nearly stoneless silty clay, with occasional gravelly particles of chert; medium crumb structure; very moist; porous and fissured; moderately high organic matter; friable; many fibrous roots; non-calcareous.
3-5 in.	Medium red silty clay with several hard sub-angular and rounded limestone fragments, varying in size from small (1 in.) to very large (upto 8 in.) below, merging with parent rock; occasional gravelly particles of chert; soil slightly less porous and apparently with low organic matter content; slightly calcareous.
5 in+	Broken limestone with some red silty clay in cracks, passing to massive limestone, with mineral veins and red staining at about 12 in.

Example of Type 2 profile (Surface soil separated from parent rock by thick layer of fragmented limestone)./ (Phot.11b,p.65).

Face of a quarry on Shute Shelve Hill, near Axbridge; situated in moderately sloping ground.

Vegetation: fairly tall, closed turf; a preponderance of herbs, Poterium sanguisorba, Filipendula vulgaris, Helianthemum chamaecistus, Potentilla erecta, Festuca ovina, Sieglingia decumbens, etc.)

Profile description.

0-4½ in.	Thick turfy mat, with thick layer of vegetable debris and a thin humus layer, overlying dark brown stoneless silty clay; medium crumb structure, with greyish faces, very loose; very moist; mellow, very porous and fissured; high organic matter; many fibrous roots; non-calcareous.
4½-18 in.	Light reddish-brown fine sandy silt, full of angular to sub-angular, small to very large limestone fragments; coarse crumb structure, firmer; very moist; fissured and fine porous; organic matter content very low; friable; a few fibrous roots above; soil calcareous, especially adjacent to rock fragments. Some of rock fragments had a slightly softened surface layer.
18-24 in.+	Massive limestone with brown and black staining.

Both Type 1 and Type 2 profile are grouped in the Lulsgate Series of the Mendip area by the Soil Survey of England and Wales (Soil Survey, unpublished data).

The frequency of occurrence of the two types of profile beneath the recorded areas of grassland may perhaps be indicated by the figures under 'Carboniferous Limestone' in Table 14.

TABLE 14

Summary of observations on the number and size of limestone fragments in the upper part of the soil profile on the recorded areas.

Number and size of fragments	Number of areas	
	Carboniferous Limestone	Oolitic Limestone
Few large fragments	17	9
Many medium "	16	12
Very many small "	15	29
Fragments not seen above 14 in.	2	0

It seems likely that most of the areas on Carboniferous Limestone with a few large fragments and some of those with fragments of medium size have a profile resembling Type 1, whereas the remainder of the areas, excluding 2 with very deep soils may well have a Type 2 profile or an intermediate variety. The occurrence of the two types is not apparently dependent on the slope of the land surface: both types were observed on gentle and on steep slopes. Their relative distribution is more probably related to the angle of dip of the rock and to local weathering properties of the limestone, as well as to topographical influence.

The Oolitic Limestone profile

Only one type of profile has been observed on the Oolite: this is characterized by a thick layer of limestone fragments between the superficial soil and the massive, unweathered limestone. This type of profile probably occurs on all recorded areas of grassland, though the areas showing only a few large stones in a brief field inspection (Table 14, under 'Oolitic limestone') may have the layer of limestone fragments of reduced thickness.

Example of soil-profile on the Oolite. (Phot.11c,p.65).

Face of a quarry near Northleach; situated in level ground.

Vegetation: ungrazed, nearly closed turf; mainly *Zerna erecta* with *Festuca ovina*, *Trifolium spp.*, *Hippocrepis comosa*, *Scabiosa columbaria*, etc; *Fissidens taxifolius* abundant.

Profile description.

0-7 in. Thin layer of vegetable debris overlying strong brown sandy clay, containing occasional sub-angular limestone fragments, ranging from gravel (1/4 in.) to small stones (1 in.), and frequent sandy particles of oolite; medium crumb structure; moist; fairly loose, porous and fissured; moderate organic matter content; friable; many fibrous roots; calcareous.

7-17 in. Medium brown clay, full of angular and sub-angular to rounded limestone fragments, loosely packed, varying in size from very small (½ in.) to medium (2-4 in.), with abundant sandy particles of oolite; coarse crumb structure; moist; firmer, fine porous and fissured; low organic matter content; friable; frequent plant roots; very calcareous; gradually merging to

17-36 in. Small to large or very large (more than 8 in.) below, bedded limestone fragments, with creamy white to yellowish-brown, very moist oolitic sand in the interstices; oolitic sand practically structureless and only contains minute quantities of clay; rock fragments have soft surfaces, and sometimes may be soft throughout.

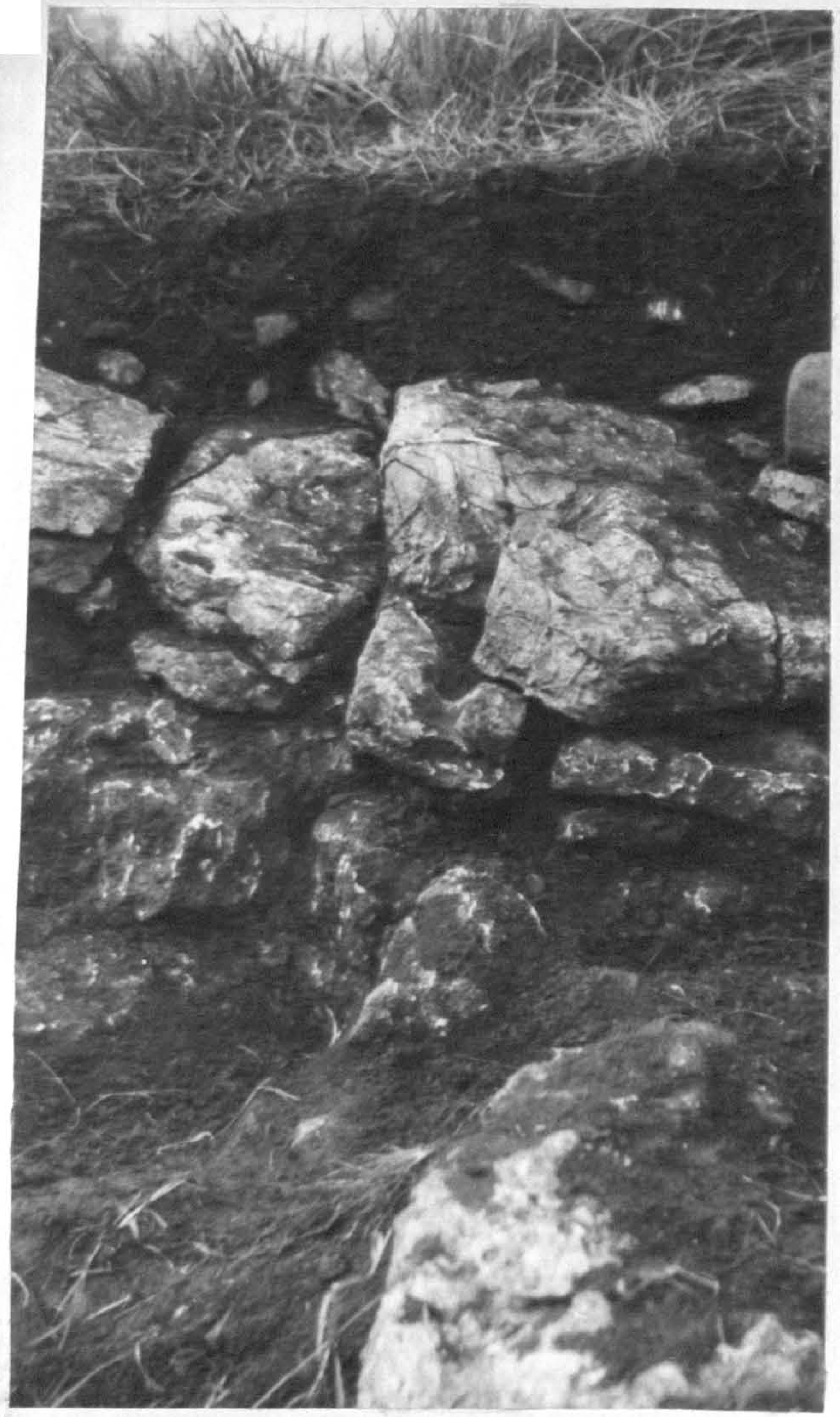
36 in. Massive, even - and current-bedded, white to yellow-brown medium textured oolitic limestone (Great Oolite)

This profile is classed in the Sherborne Series by the Soil Survey of England and Wales (Soil Survey, unpublished data).

The main differences to be observed between the profiles of the two limestones are as follows:

Shape and distribution of rock-fragments.

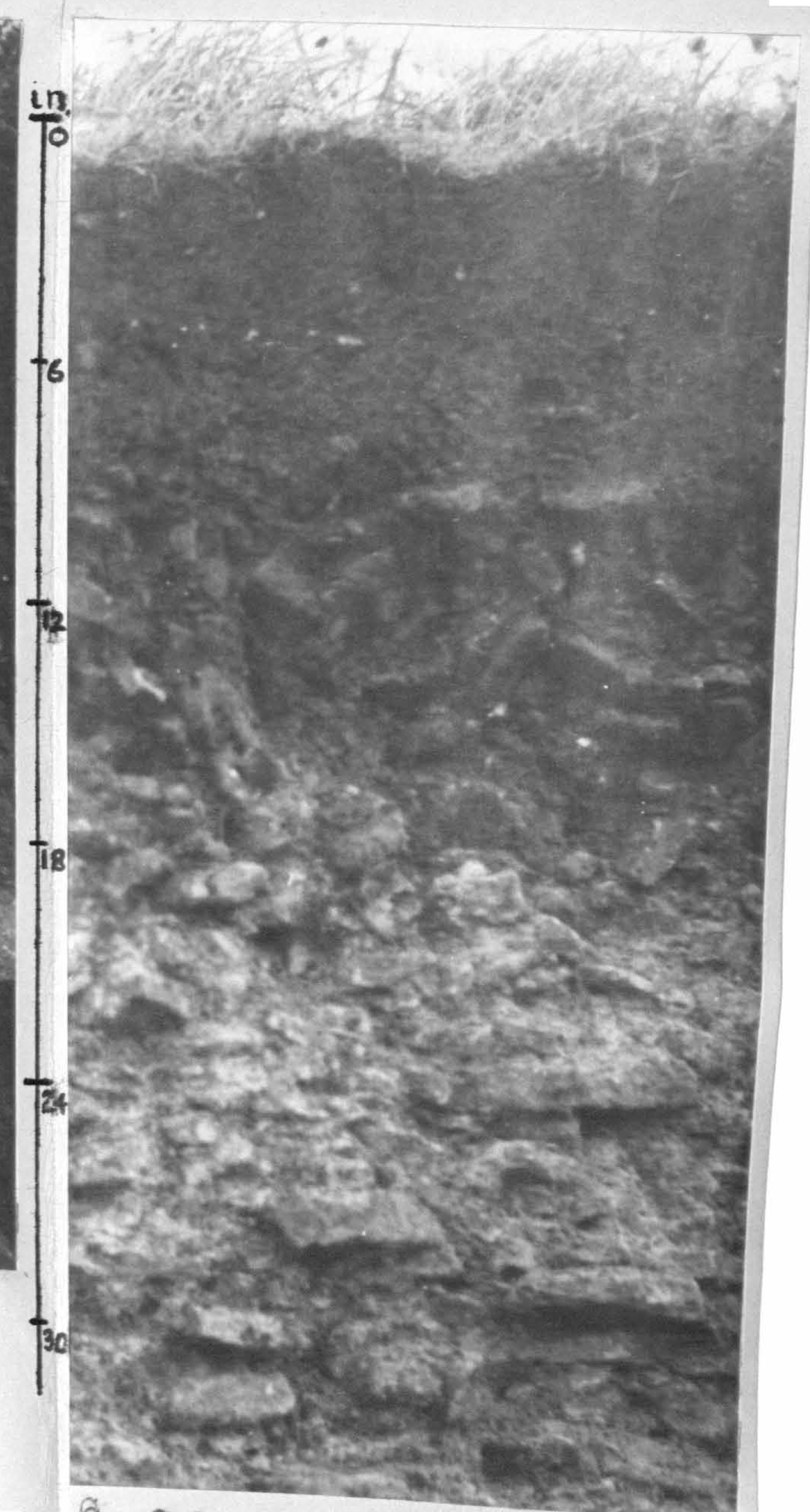
On the Oolitic limestone there is a gradual appearance of rock-fragments down the profile, and a steady increase in size and density over a considerable distance (2 or 3 feet); fragments often extend right to the surface. Oolitic fragments, mainly small or very small above, becoming medium to large lower down the profile are angular or sub-angular to rounded, but, owing to the soft nature of the rock, do not have harsh edges. The fragments are loosely packed and surrounded by conspicuous amounts of interstitial soil and crumbled limestone to a depth of about 2 feet.



A. Type 1. Thin transition zone of limestone fragments from soil to parent rock.

B. Type 2. Thick transition zone of rock fragments.

Phot. 11. A & B. Carboniferous Limestone profile.



C. Oolitic Limestone profile.

On the Carboniferous Limestone there is a more sudden appearance of rock fragments down the profile and a more rapid increase of their size and density; the layer of fragmented rock is thinner than on the Oolite (about 18 in. in Type 2 profile) and is often little more than a single layer of moderately large and irregular limestone fragments, resting above the parent rock (Type 1 profile). The surface soil is generally free of stones but may contain scattered small fragments of chert. Carboniferous Limestone fragments, mainly medium or large in size, but grading to small in Type 2 profile, are angular or sub-angular or occasionally worn smooth by weathering (cf. Phot. 11, Type 1 profile). Because of the hardness of the rock most of the fragments have harsh, almost flint-like edges. They are more closely packed, especially in the lower part of the profile, and have correspondingly less interstitial soil than on the Oolite.

The differences in the rock skeleton of the soil profiles result from the different weathering properties of the two limestones which are in turn dependent on differences in the physical, and, to some extent, the chemical properties of the two rock-types. The physical and chemical properties of the two limestones of importance in determining weathering behaviour are listed in Table 15.

TABLE 15

Physical and chemical properties of the Carboniferous and Oolitic Limestones important in determining weathering behaviour.

Carboniferous Limestone	Oolitic Limestone
Texture and Mineral Composition ;	
Medium - or fine-textured grey limestone, consisting mainly of a highly compacted matrix of mutually interferent calcite crystals, with impurities of quartz and other mineral particles. Commonly recognizable organisms are few or none, but coarse shelly varieties sometimes occur. Nodules of chert and mineral veins are frequently present in the rock.	Coarse - or medium-textured, cream to yellow-brown limestones, characteristically containing sphaeroidal or ellipsoidal grains of calcium carbonate, about 1 mm. diameter (oolites). Frequently (e.g. in most free-stones) the bulk of the rock consists of oolites set in a crystalline matrix of calcite stained with iron-compounds. In the less pure types there is proportionately more matrix which is often earthy or rubbly, and containing considerable amounts of quartz, iron-compounds and argillaceous matter.

Mechanical properties:

Characteristically hard and very compacted rock	Typically softer and less compacted than the Carboniferous Limestone.

Compare density and crushing-load for typical rock samples (data from North, 1930.).

	e.g. Hopton Wood Stone.	e.g. Corsham Down Stone (Great Oolite)
Density	2·54	2·06
Crushing load (tons per square foot):	806	94·5

Gross chemical composition: Analyses of typical rock-samples (quoted from North, 1930)

	Carboniferous Limestone, S. Wales.	Great Oolite (Bath stone)
	%	%
$CaCO_3$	97·40	95·55
$MgCO_3$	1·43	0·67
FeO, Fe_2O_3	0·27	1·22
Al_2O_3	0·10	0·46
SiO_2	1·60	0·42
Na_2O	-	0·44
P_2O_5	trace	-
SO_3	0·035	trace
Cl	-	0·03
H_2O	-	0·88

Analyses of other rock samples (North, 1930; Soil Survey, unpublished data)

Show the following features:

Carboniferous Limestone is in general very pure, with calcium carbonate content usually around 98-99%; a number of types are dolomitized, with $MgCO_3$ replacing some of $CaCO_3$ component; a few impure varieties contain moderately large amounts of silica.

Oolitic limestone is generally less pure, with $CaCO_3$-contents usually 93-96%; dolomite is present only in relatively small amounts (upto 3%).

The data quoted by North (1930) are from analyses of building stones, which usually represent the purest varieties of limestone, and, on the Oolite, where rock strata are very varied compared with the more uniform Carboniferous Limestone, some of the earthy and rubbly varieties are considerably less pure than the quoted figures indicate.

The hard compact relatively homogeneous Carboniferous Limestone, with but few joints or irregularities in its structure, weathers slowly and regularly and it is fractured infrequently by the forces of weathering. The softer, less compacted Oolitic limestone, very heterogeneous through the presence of oolites, weathers more rapidly and less regularly and the massive rock is easily fragmented. In addition the greater porosity of the Oolitic Limestone allows much more of drainage water to seep through the whole rock structure, thus chemical weathering may occur within the mass of the rock as well as at the surface. On the Carboniferous Limestone water tends to drain mainly along vertical and horizontal joints in the rock-strata, so that chemical weathering proceeds largely at the surfaces of the fragmented rock.

The differences in the initial processes of weathering of the bare rock are strikingly demonstrated in a comparison of the dry stone walls on the two limestones. The stones are rarely fractured in walls on the Mendips, whereas on the Cotswolds, the stones are cracked in most walls and are quite often reduced to a crumbled condition.

In the soil profile the more rapid and more extensive weathering of the Oolitic limestone gives rise to a thicker layer of limestone fragments than the Carboniferous Limestone. In Type 2 profile of the Carboniferous Limestone the thickness of fragmented rock is intermediate between Type 1 profile of this limestone and the Oolite profile. The thicker layer of fragments in Type 2 profile, compared with Type 1 of the Carboniferous Limestone, may be associated with a softer, more rapidly weathering variety of limestone (cf. softened surface of rock fragments, in profile description p.60.)

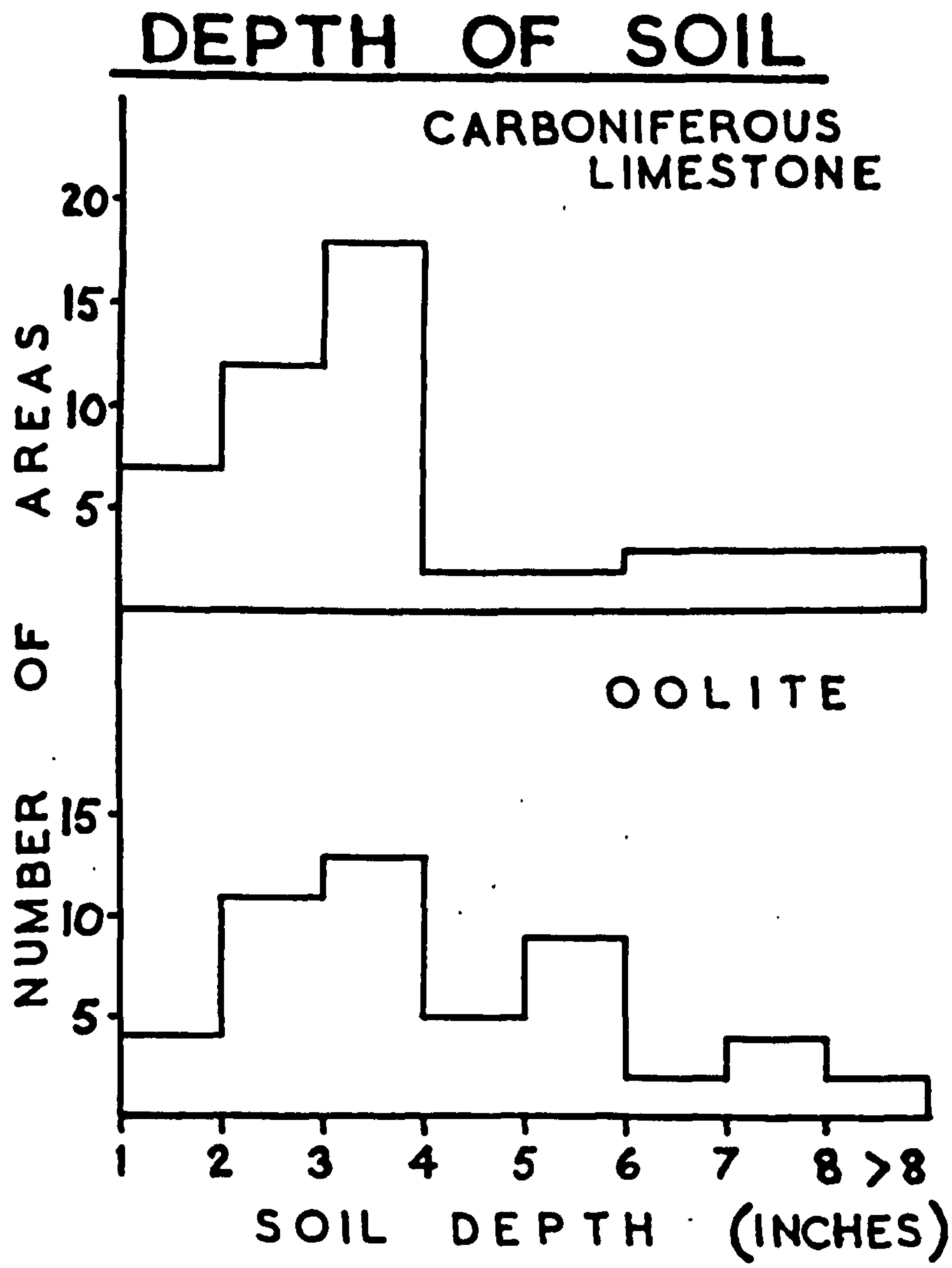


Figure 13. Soil depth in 50 grassland areas on each limestone.

Soil Depth.

In general the depth of soil is greater over the Oolitic limestone. Thus the proportion of recorded areas on the Oolite with soil-depth more than 4 in. is greater than on the Carboniferous Limestone. (cf. Fig.13). The greater soil depth on the Oolite is related to the comparatively less pure limestone and to the greater speed of rock-weathering. The larger amounts of interstitial soil between the Oolitic rock fragments may also be related to these two factors.

Soil depth is generally very even over an area on the Oolite, but on the Carboniferous Limestone it may be irregular, with frequent outcrops of bare rock. This is a consequence of the resistant properties of the Carboniferous Limestone rock which can long remain close to the soil surface, or exposed completely, without becoming appreciably weathered.

Owing to the relatively slow rate of weathering on the Carboniferous Limestone, erosion forces have a greater effect on soil depth, which is therefore more dependent on local pedogenic conditions (e.g. angle of dip of the rock, variety of limestone) than on the

Oolite. On the same slope an outcrop of a hard variety of Carboniferous Limestone may carry a shallow soil adjacent to a deeper soil overlying an outcrop of a more rapidly weathering variety.

Nature of the soil.

The soil itself is conspicuously different on the two limestones. The most striking difference is in colour: soils on the Carboniferous Limestone are typically red or red-brown, occasionally grey-brown or dark brown, but always with a discernible reddish tinge. On the Oolite, soils are generally brown or dark brown, with some of the heavier clays yellowish-grey or dark grey in colour; some oolitic soils are light brown or rusty brown, but there is never any reddish colouration. On both limestones the soil is generally uniform down the profile when of shallow depth but the deeper soils show some zonation. (Cf. profile descriptions, pp.60,63.). In these instances the soil below is lighter in colour, more compacted and apparently of very low organic matter content, becoming darker and less compact in the main rooting layer. Sometimes a spongy surface layer of humus is present, overlain by undecayed vegetable debris.

A recognizable litter layer is more frequently seen on the Carboniferous Limestone (21 times), where it is often of considerable thickness (½-2 in.); on the few (11) Oolite areas with an identifiable litter layer, it is generally thin and rarely exceeds ½ in. There are considerable differences in the texture of the two soil-types. Oolite soils vary from light sandy loams to heavy clays, but are most frequently somewhat sandy medium clays. The presence of sandy particles of oolitic limestone is a characteristic feature; these are present in reduced amounts, or absent, only in very deep soils or in the heavier clays. On the Carboniferous Limestone, the soil is generally of a light or medium silty texture, occasionally sandy and sometimes of a heavier clay texture. The main rooting layer rarely contains sandy particles of unweathered limestone, but often shows small scattered fragments of chert, which have been left unweathered in the soil after solution of calcium carbonate from the remainder of the parent rock. (cf. mineral composition of rock, Table 15, p. 66.).

Probably on account of texture differences, Carboniferous Limestone soils are much stickier when wet and appear to dry in air more quickly than the Oolitic type. Further, soils on the Carboniferous Limestone generally appear more compacted and thus less porous, though some of the heavier Oolitic clay soils are fairly compacted.

The differences in texture are mainly related to the weathering of the impurities of the two limestone rock-types, though it seems that not all soils are entirely sedentary in origin. Thus in the Cotswolds, especially in the south, some of the steeper slopes outcropping below clay formations (e.g. the Fuller's Earth formation), may have been contaminated by a clay downwash, and on some of the maritime slopes on Carboniferous Limestone e.g. Brean Down and Middle Hope, the soil is full of sand blown from wide beaches (cf. mechanical analysis section p. 93.). It is possible that on other parts of the Carboniferous Limestone outcrop the soils have been augmented by wind-borne deposits (Soil Survey, 1950, 1954.).

Carbonate content.

There is a very marked difference in carbonate content of the two soil types. The majority of Oolitic soils give a violent effervescence with dilute HCl, while very few

Carboniferous Limestone soils show any reaction. Thus of 36 Carboniferous Limestone soils tested only 3 gave an appreciable reaction; of 44 Oolitic soils tested, 5 were without reaction and 5 others gave a slow effervescence.

The excess of free carbonate in Oolite soils arises at least partly from the manner of soil formation on this limestone. The general presence of sandy particles of oolitic limestone is undoubtedly related to the rapid weathering of the rock, though the proximate reason for their uniform distribution in the soil is not clear; possibly the calcite matrix of the oolitic rock is rapidly removed in weathering leaving a mass of oolitic grains, which may be relatively slow-weathering and become dispersed in the soil.

On the Carboniferous Limestone the soil is generally quite free of carbonate even when adjacent to limestone fragments; the rock fragments are too large and slow-weathering to maintain the presence of carbonate in the bulk of the soil.

There are indications from inspection of the vegetation-cover that soils on Carboniferous Limestone with small rock-fragments, while containing no free carbonate are richer in bases than those with large fragments, presumably because of the quicker weathering of limestone associated with the presence of many small rock-fragments. Thus of 11 areas on the Carboniferous Limestone showing limestone fragments of moderately large size and a depth of soil less than 5 in. 7 had a conspicuous abundance of somewhat calcifuge species and a low abundance of calcicoles, whereas areas with smaller rock fragments generally showed a prevalence of calcicolous species. It is significant that a shallow profile with a few large limestone fragments occurs beneath limestone heath vegetation in several places on the Mendips.

Plant roots and soil moisture retention.

In both soil types the upper 3-6 in. are thickly permeated by plant roots; the main rooting layer is more frequently deeper on the Oolitic limestone, probably corresponding to the greater depths of soil here.

On the Carboniferous Limestone, plant roots often appear thin and wiry and are only loosely bound to the soil, whereas on the oolite they are of more fleshy appearance and are more intimately bound to the soil aggregates.

The appearance of the plant roots was probably related to the field moisture-contents of the soil at the time of recording. During rainless periods, the soil of the rooting-layer appears to dry out very quickly on Carboniferous Limestone, whereas all but the most sandy of Oolitic soils retain perceptible moistness for long periods.

Price (1948) notes the rapid drying-out of Carboniferous Limestone soil, whereas he observes that the soil on the Cotswold Oolite has remarkable powers of water retention. The favourable water-retaining properties of the soil of the Cotswold Hills, inspite of its shallow depth and stony character is frequently referred to by agriculturists e.g. Twyman (1954).

In conclusion, it maybe noted that the typical profile on the Oolitic limestone is a rendzina; there is free carbonate throughout the profile and an increasing size of limestone fragments with depth; the soil has a grey-brown or brown colour, never reddish-brown and the organic matter is dark-coloured (Robinson 1949).

On the other hand, Type 1 profile of the Carboniferous Limestone corresponds very closely to the description given (Robinson, 1949) for the terra rossa soils, characteristic of limestones in the Mediterranean region. Thus on the Mendips, Type 1 profile consists of a red or red-brown, medium-heavy soil passing abruptly to the limestone rock below without any marked zone of transition. The soil typically contains no free carbonate, except for isolated fragments which because of slow-weathering properties, are unable to affect markedly the base-status of the surrounding soil. Type 2 profile resembles Type 1 but has a thicker transition zone of limestone fragments between the soil and the parent rock. Type 2 can be regarded as an intermediate variety of limestone profile: it has a limestone skeleton characteristic of a rendzina, but shows base-unsaturation and red-coloured soil, characteristic of a terra rossa soil.

Robinson (1949) classes profiles on Carboniferous Limestone in Wales with the red-brown limestone soils of the terra rossa group. McLean (1935) has also noted the resemblance of the S.Wales Carboniferous Limestone soils to the terra rossa type.

2. Laboratory investigation of the soil.

The aim of the laboratory investigation was to compare some of the characteristic properties of the two soil types which seemed most likely to have a direct influence on the composition of the vegetation cover, through the effect on plant growth.

The chemical environment provided by the soil was investigated by the determination of pH and by an estimation of the levels of available plant nutrients. The physical properties investigated were those relating to the texture of the soil (Mechanical composition; organic matter content), and to its effective water-retaining properties (Hygroscopic coefficient; moisture equivalent; permanent wilting percentage).

Method of sampling

Samples of soil for analysis were obtained from widely scattered areas of the two types of calcareous grassland. Situations were selected to include the main variations in soil appearance, site characters and in floristic composition encountered on the two limestones.

On the selected area soil was sampled from the main rooting layer (1-3 or 4 in. depth) at 10 more or less evenly scattered points. The soil so obtained was well mixed on a piece of sacking, any coarse roots or large rock fragments being removed. About 2 lbs. of soil, representing the whole of the area, were subsampled to a tin with a tightly - fitting lid for transport to the laboratory.

Preparation of the samples for analysis

The treatment of the field-samples and a number of experimental techniques followed the methods recommended by Piper (1942).

Measurements of pH were made on freshly-sampled field-moist soil. For all other determinations air-dried soil was used. The sample was air-dried in a layer ½-1 in. thick on paper. The air-dry soil was ground down in a mortar and sieved through a 2 mm. mesh screen; a wooden pestle was used for grinding the soil so that there was no breakdown of any rock fragments present. The material passing through the sieve ('fine earth') was stored in a tin and was the fraction used for analysis. The small stones and plant roots remaining on the sieve were weighed before discarding, to give the fraction of 'stones and gravel' in the original sample.

Experimental Methods and results.

The results considered here, unless otherwise stated, are from 20 soil samples of each limestone-type. Complete analytical data for these samples are given in full in the Appendix.

Except where otherwise stated results are expressed as % by weight of oven-dry soil. Moisture contents of the soil were determined by drying at 105°C for 24 hours.

(1) Determination of pH. (Piper 1942)

Measurements of pH were made under standard conditions, using a 1:5 soil:water suspension, 20 gm. freshly-sampled soil and 100 ml. distilled water were mechanically shaken for 1 hour at room temperature and the pH of the suspension was quickly measured using a glass electrode calomel half-cell electrode system and pH-meter.

The pH of some samples was also measured with the electrodes in direct contact with the field-moist soil.

Results:

The pH-values for 32 soils from each limestone are summarized in Fig.14.

Carboniferous Limestone soils in general show a distinctly lower pH. The great majority give values

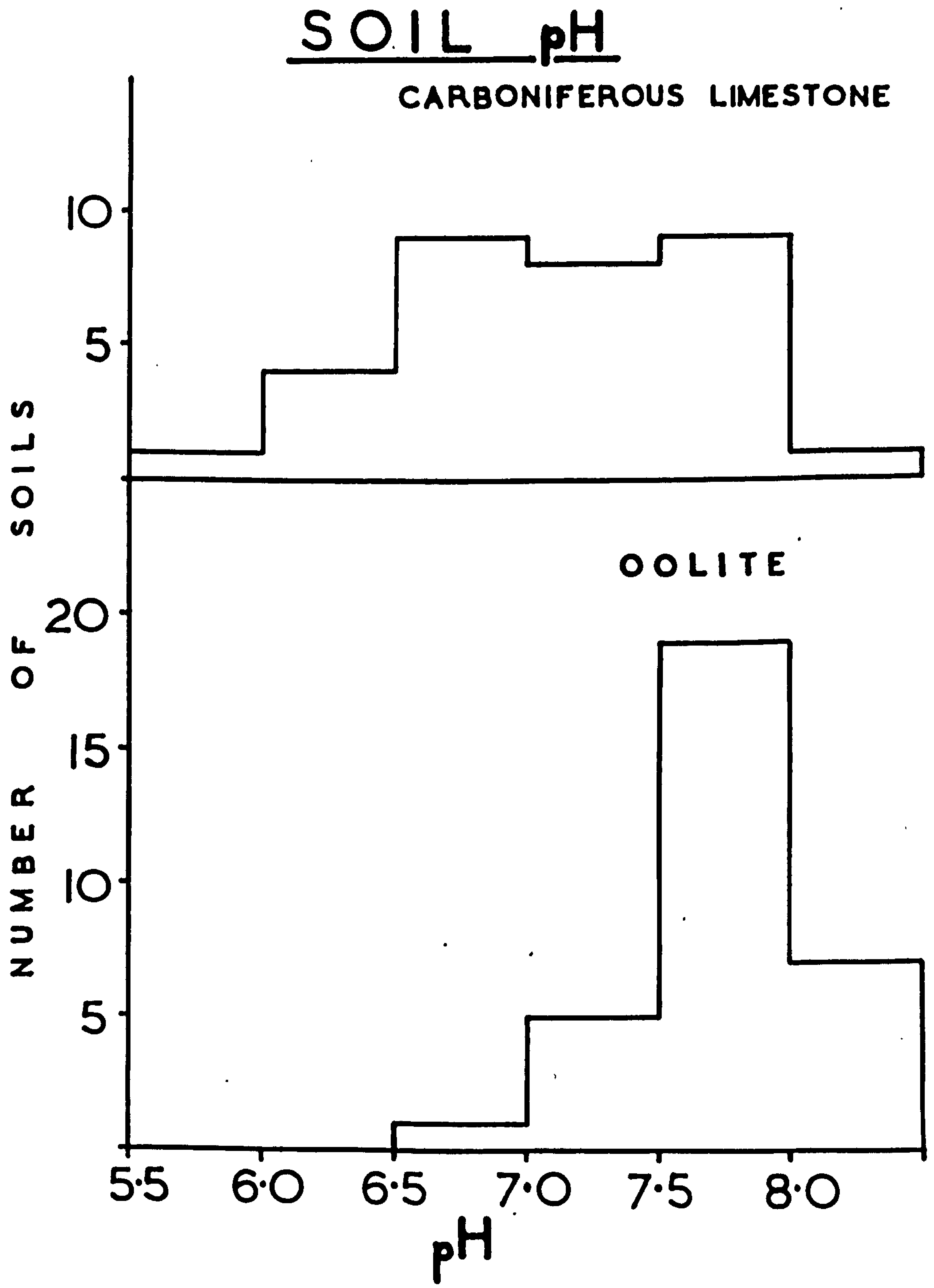

SOIL pH
CARBONIFEROUS LIMESTONE
OOLITE
NUMBER OF SOILS
10
5
20
15
10
5
5·5
6·0
6·5
7·0
7·5
8·0
pH

Figure 14.

between 6·5 and 7·5, frequently below 7·0. Several shallow soils on south-facing slopes have pH above 7·5, but only one soil showed a pH above 8·0. This was from the area at Draycott where the high pH is at least partly due to the presence of particles of burnt lime in the soil from an old liming-treatment. On two areas with deep soils the pH was close to 6·0.

On the other hand most soils on Oolitic limestone, with their high content of free carbonate, show pH 7·7-8·1. Several stoneless clay soils have a somewhat lower pH : 7·4-7·6, but only two clays and one deep loam had pH close to 7·0. There was evidence of leaching in the floristic composition of the latter 3 areas.

From pH-measurements with electrodes inserted directly into the soil at field-moisture content, there are indications that the effective pH of the soil in contact with the plant roots is less than the values recorded from soil suspensions (cf. Table 16). The discrepancy varies with moisture-content of the soil and is greater when the soil is drier.

TABLE 16.

Comparison of pH of 1:5 suspension and of field-moist soil.

	Field-moist soil	1:5 Suspension
Carboniferous Limestone		
Shallow soil (2 in. depth), valley near Charterhouse.	6·74	7·54
Deeper soil (4 in. depth), Dolebury Warren.	6·05	6·59
Oolitic Limestone		
Shallow stony soil, Eastleach.	7·46	8·04
Deep stoneless soil, Upper Slaughter.	6·82	7·40

(ii) Proportion of 'stones and gravel' in the soil samples.

Figures for the percentages (air-dry basis) of 'stones and gravel' in 26 samples of each soil-type are summarized in Fig.15.

In samples from Carboniferous Limestone the 'stones and gravel' fraction varied from practically none (0·05%) to 24·7%; in soils from the Oolite it varied from 0·5% to almost half the total weight of the sample (49·7%).

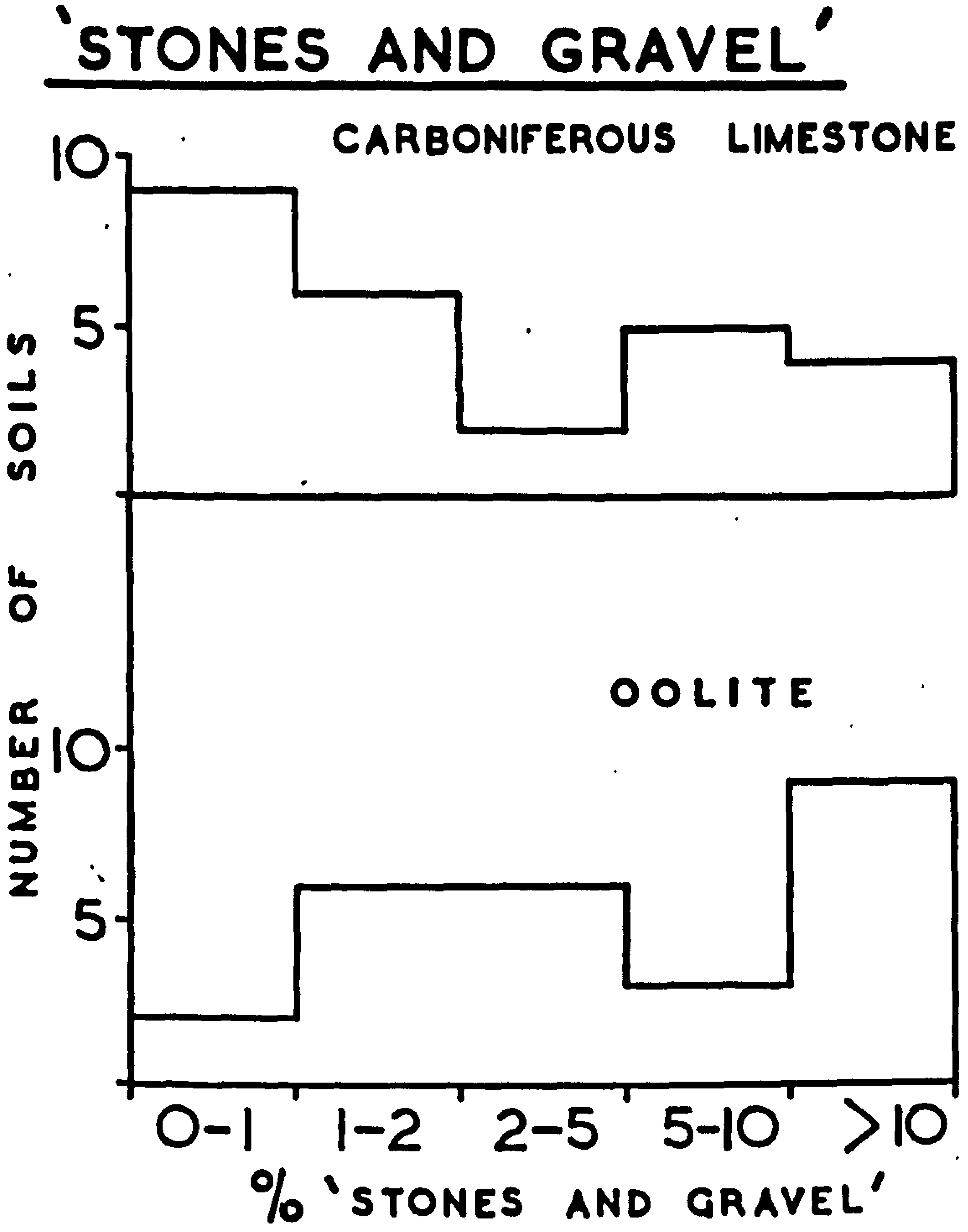


Figure 15. Comparison of the 'stones and gravel' fraction in soil samples of the two limestone types.

The smaller frequency of negligible amounts of 'stones and gravel' (less than 1%) on the Oolite is a reflection of the more frequent extension of rock-fragments into the main rooting layer on this limestone.

The Oolitic 'stones and gravel' always gave effervescence with dilute HCl, while in the Carboniferous Limestone samples this fraction sometimes contained mainly chert or quartz fragments, without free carbonate.

(iii) Determinations of the levels of available plant nutrients in the soil.

The system of rapid chemical tests developed by Morgan (1942) was employed to obtain estimates of the amounts of available plant nutrients in the soil.

The experimental technique used here closely followed that described by Morgan (1942).

In the preparation of the soil extract, the simple percolation technique was used: 4 grams air-dried soil were extracted on a filter-paper with 10 ml. Morgan's reagent (10% sodium acetate solution buffered to pH 4·8 with acetic acid). The extract was poured back through the soil mass twice more to ensure uniform extraction. Results were found to depend on whether air-dry or field-moist soil was used; lower test-readings were obtained for some radicals (e.g. K) when moist soil was extracted. These differences were noticed even if a proportionately higher weight of moist soil was used, to allow for its moisture content.

The test readings for some radicals varied with the soil: liquid ratio; a 4:5 ratio (8 gm. soil : 10 mls. liquid) gave higher readings, and a 1:5 ratio (2 gm : 10 ml.), lower readings, compared with a 2:5 (4 gm. : 10 ml.) soil: liquid ratio. Relative test readings for different soils are more easily compared at high nutrient levels, but the 2:5 ratio was adopted as standard, since higher ratios gave insufficient amounts of extract with the more retentive soils.

The simple percolation method of extraction was compared with a shaking method for one series of samples. In the shaking method extensively used by the National Agricultural Advisory Service, 10 gm. air-dried soil and 50 ml. Morgan's reagent are mechanically shaken in tightly-stoppered bottles for 15 min. The shaking method showed no distinct advantage over the simple percolation technique. Values for some radicals e.g. PO_4, Mn, were higher for some soils with the shaking method, possibly because of a more thorough extraction of the soil particles, since a similar effect was observed when the soil in the percolation method was extracted six times instead of the normal three.

In the preparation of test-reagents and standard solutions, and in the conduct of the individual tests, the methods of Morgan (1942) were followed exactly. Extracts from six soils, three from each limestone, were tested simultaneously on a spot-plate or in Wassman tubes (8x1 cm.). The dropper pipettes used delivered approx. 30 drops per ml.

The radicals tested were nitrate, ammonium, phosphate, potassium, calcium, magnesium, aluminium and iron.

The test-readings were recorded as numerical values the approximate significance of which in the nutrition of the plant has been based (Morgan, 1942) on crop requirements in a wide variety of soils. The meanings attached by Morgan to the numerical test-values are listed in Table 17.

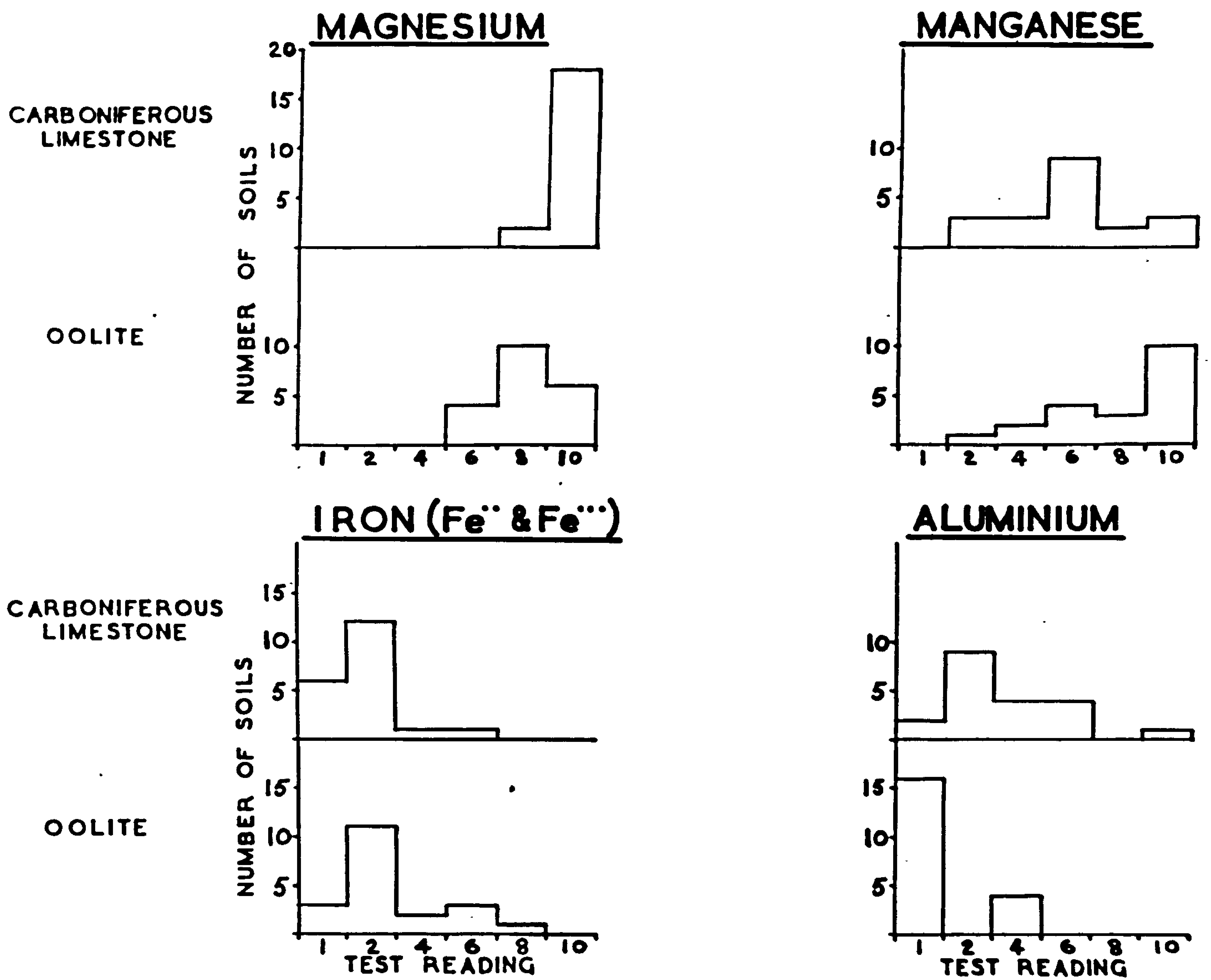


Figure 16. Results of Morgan tests.

TABLE 17

Test-reading.	Level of nutrient available in the soil.
1	Very Low
2	Low
4	Medium
6	Medium High
8	High
10	Very High

Results

The results of tests on the extracts of 20 soils from each limestone are summarized in histogram form (Fig.16-18).

From estimates of the amounts of available plant nutrients in the two series of soils, obtained by Morgan's method, the following features are apparent:

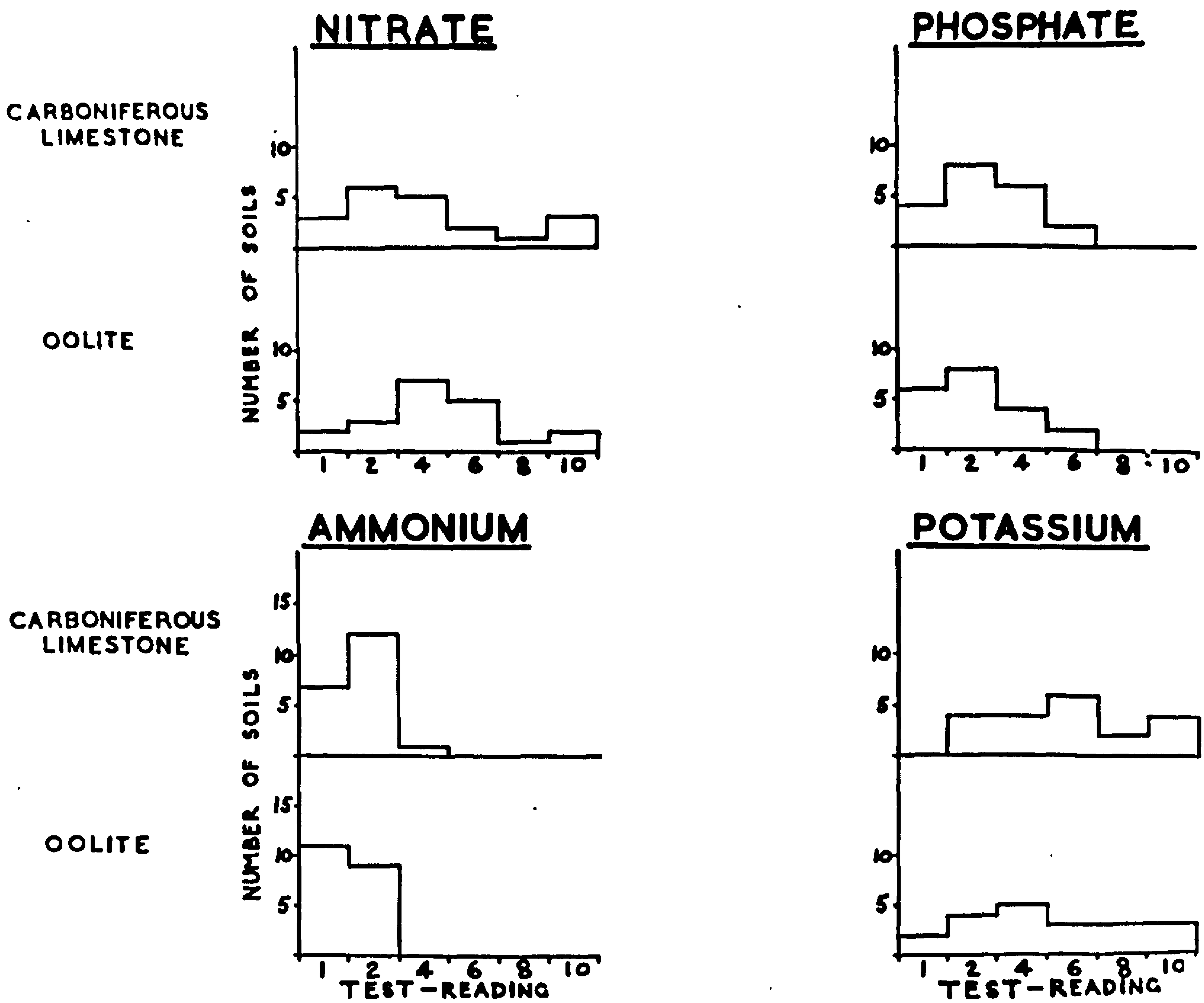


Figure 17. Results of Morgan tests.

While the levels of nitrate, ammonium, and phosphate have a similar range for the two soil-types, a marked difference in the level of available calcium may be observed and less distinct differences in the levels of the other radicals tested.

<u>Calcium</u>

The great majority of Oolite soils have very much more available calcium than typical Carboniferous Limestone soils, and characteristically are probably base-saturated. Four Oolite soils, pH 6·89-7·40, show levels of calcium, which are much lower than the remainder of samples from this limestone, and which are roughly equivalent to the highest levels obtaining in Carboniferous Limestone soils.

Although the Carboniferous Limestone soils show varying degrees of calcium unsaturation, they are by no means deficient in this element. Thus all soils from the Carboniferous Limestone gave a test value 10 when 10 drops of soil extract were tested. However, when the extracts were diluted and re-tested, (1 drop extract, 9 drops Morgan reagent), the difference between the two soil-types was apparent. Whereas at this dilution

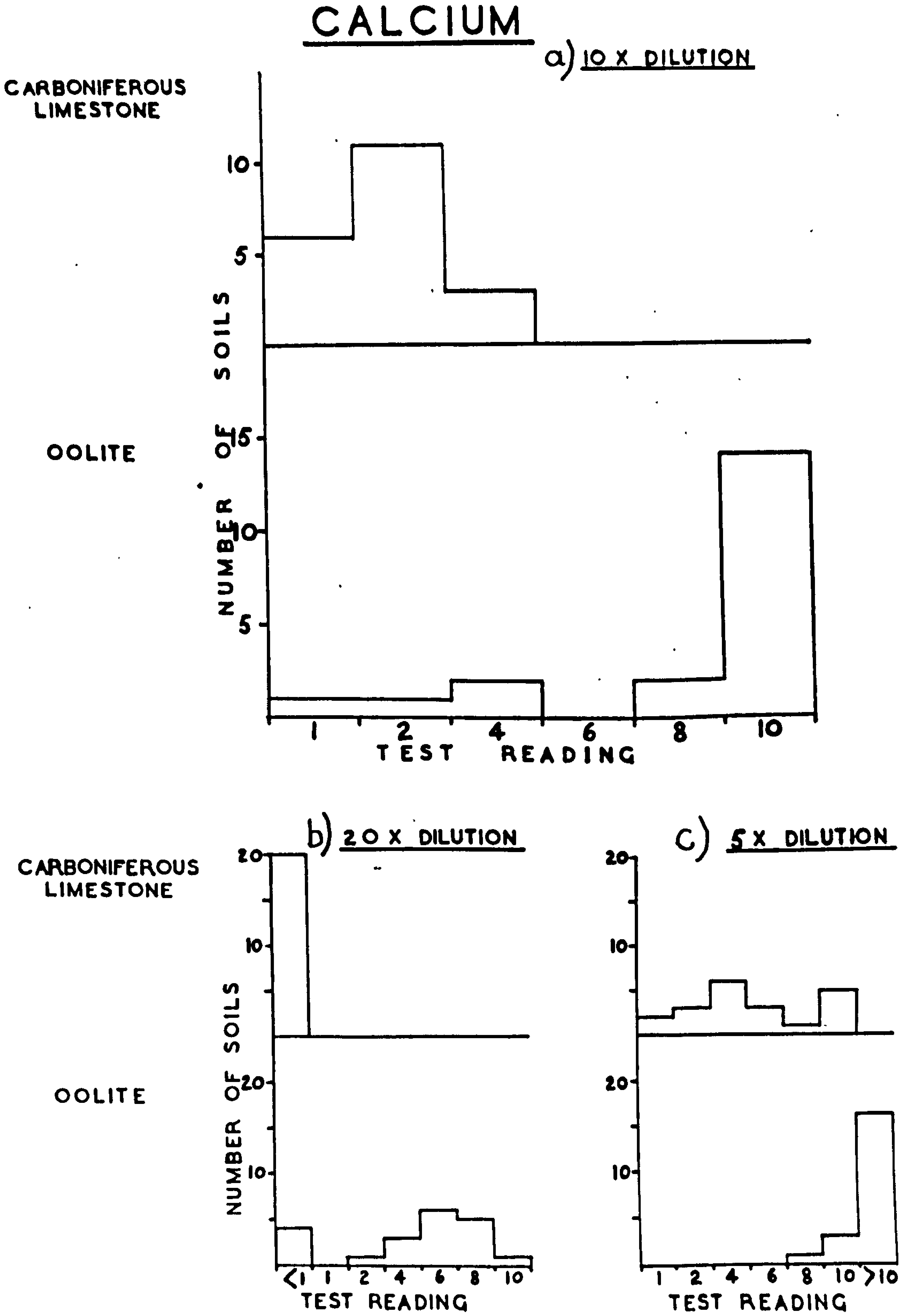


Figure 18. Results of Morgan tests.

Carboniferous Limestone soils had calcium test values varying from 1-4, only the four Oolite soils referred to above showed comparable levels; the remainder had test values 8 or 10 or above 10. (Fig.18a.) Using extracts diluted 20 times, Oolite soils gave a range of test-values (Fig.18b.); a comparable range of values was obtained for Carboniferous Limestone soils, when 5 times - diluted extracts were tested. (Fig.18c.).

It is noteworthy that Carboniferous Limestone soils which contain free carbonate do not have a calcium-level higher than normal; thus for the Draycott soil containing particles of burnt lime, the extract gave test-value 2 at 10 times dilution, and 8 at 5 times dilution, results similar to five other soils from the Carboniferous Limestone.

Other elements.

The levels of radicals other than calcium are variable in both soil-types, but differences in some elements are apparent (Figs.16,17.); these are summarized in Table 19 (p.101.).

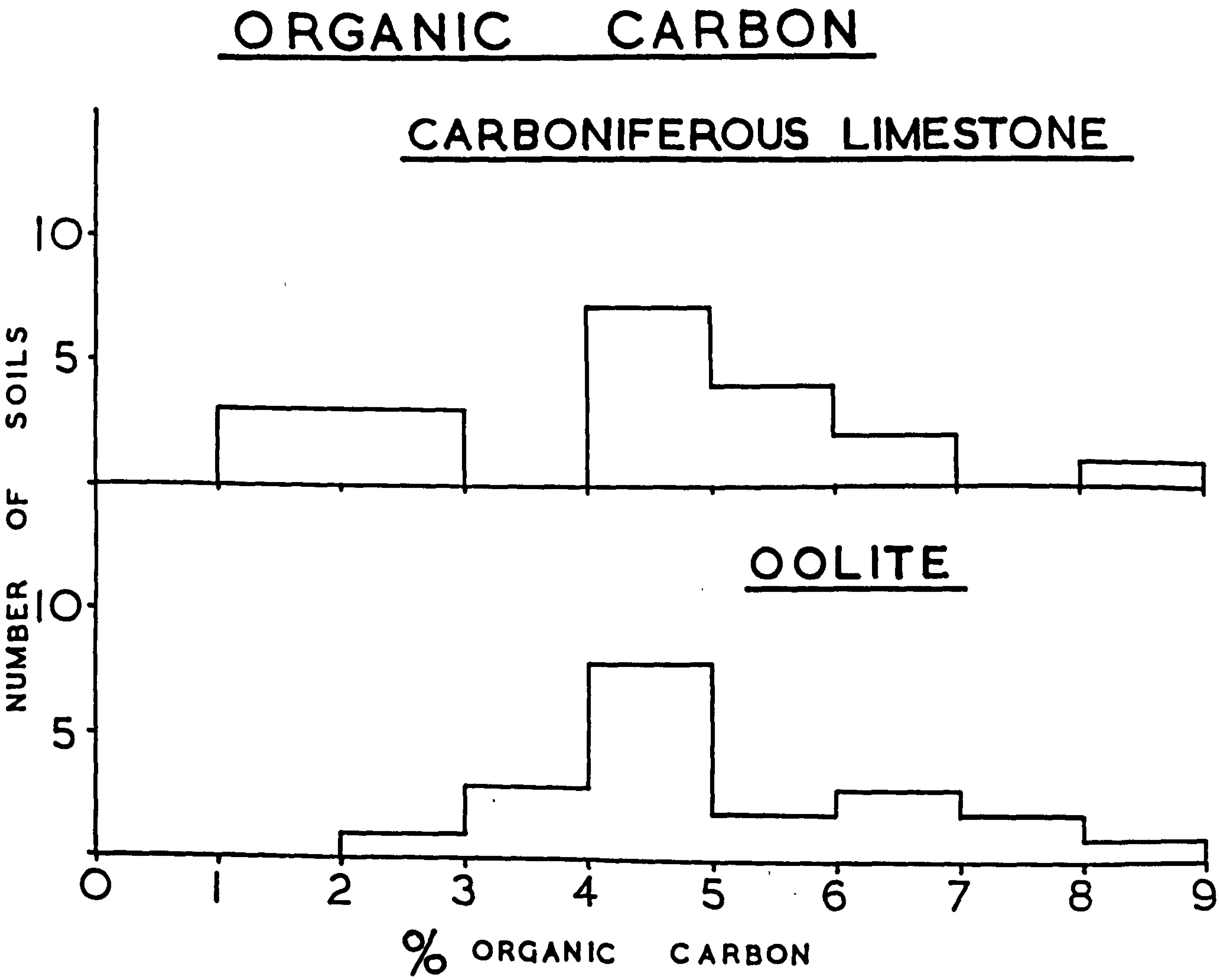

ORGANIC CARBON
CARBONIFEROUS LIMESTONE
OOLITE
NUMBER OF SOILS
10
5
10
5
0
1
2
3
4
5
6
7
8
9
% ORGANIC CARBON

Figure 19.

(iv) Organic matter.

An estimate of organic matter in the soil was obtained by the determination of organic carbon present, using Walkley and Black's method. The soil is treated with potassium dichromate and conc. sulphuric acid, and the excess of oxidising agent is determined by titration with ferrous sulphate solution. The experimental details quoted by Piper (1942) were followed, except that a fresh solution of ferrous sulphate was made for each series of determinations, instead of using a stock solution stored in an atmosphere of hydrogen.

Results.

The results are expressed as percentage organic carbon (Walkley and Black values) in the soil.

The organic carbon values for 20 soils from each limestone are summarized in Fig.19.

There are no very marked differences in organic matter content of the two soil-types, though rather more Oolitic soils show high levels and more Carboniferous Limestone soils have low levels of organic matter. The Carboniferous Limestone soils with very low organic matter were mainly from areas with deep soil, which contained a high proportion of sand (combined coarse and fine fractions) and a calcium-content lower than normal.

(v) Mechanical analysis

The method of Troell (1931), using hypobromite solution, was employed for the oxidation of organic matter and the dispersion of the soil particles, so that carbonate-containing fractions were included in the analysis. The determination of the fractions in the soil suspension followed the normal International Method (Agricultural Education Association, 1928).

Results.

Examples of mechanical analyses of the two soil types are given in Table 18.

TABLE 18

Specimen mechanical analyses of the two soil types.

	Clay	Silt	Fine Sand	Coarse Sand
Carboniferous Limestone soil:				
Sandy loam, Winscombe Hill.	16·56	24·35	35·10	12·91
Clay loam, Priddy.	37·63	19·14	29·69	1·39
Oolitic Limestone soils:				
Typical sandy clay, Hawkesbury Upton.	40·26	19·06	20·69	12·14
Stoneless clay, Marshfield.	51·58	19·64	20·48	2·02

The results for 20 soils of each limestone type are summarized in Fig.20.

There are important differences in the mechanical composition of the two soil types; the most marked of these are in the clay and sand-fractions.

Clay. The clay-content is typically much higher in Oolitic soils. The average clay-content of 20 soils from this limestone was 39% and only 7 soils showed clay less than 35%; 6 of the latter contained high

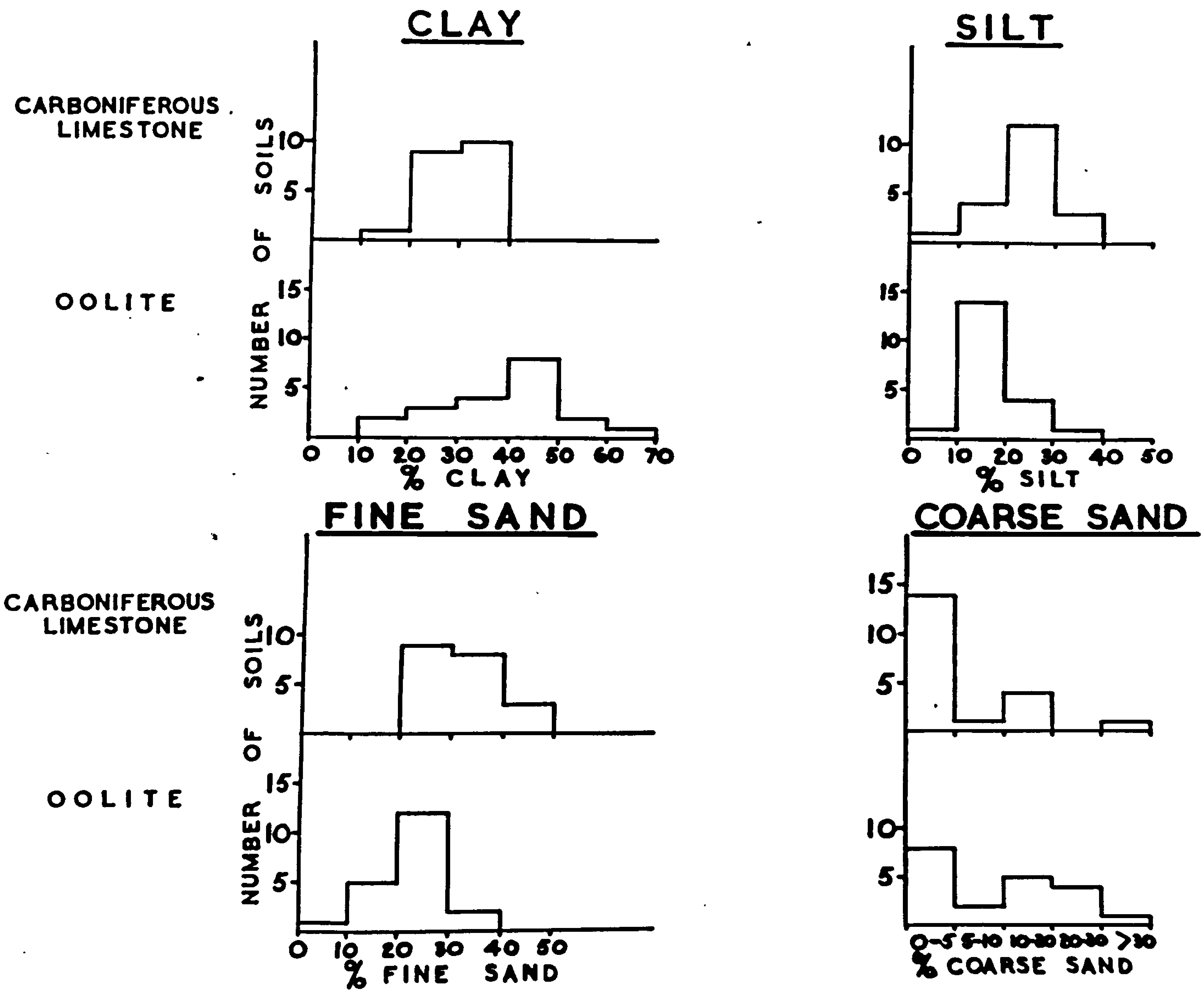


Figure 20. Comparison of the mechanical composition of 20 soils from each limestone.

sand-fractions, of unweathered limestone. On Carboniferous Limestone the average clay-content of 20 soils was 30% and only 5 soils had more than 35% clay; the maximum clay-content observed was 39%.

Silt. The silt-fraction is in general higher in Carboniferous Limestone soils; in 20 soils from this limestone silt varied from 8·13 to 34·69%, average 23%, whereas in 20 Oolitic soils this fraction ranged from 7·41 to 33·29%, average 18%.

Fine sand. There is generally a much higher fine sand fraction in Carboniferous Limestone soils; in this soil type fine sand averaged 33% and was frequently around 40%; only three soils contained less than 25%. In Oolitic soils the average fine sand content was 22% and only five soils contained more than 25%.

Coarse sand. The coarse sand fraction is more frequently high in Oolitic soils, whereas this fraction is typically low in Carboniferous Limestone soils. Of the Carboniferous Limestone soils with a high coarse sand fraction, three were from moderately steep areas with shallow soil, one from an area with an outcrop of very shelly rock and the other from the maritime slope at Middle Hope, near Weston, which has accumulated sand blown from the beach: the combined sand fractions of this soil total 62%.

Acid tests on the separated sand-fractions showed that, except for four leached soils, both fine and coarse sand fractions of Oolitic soils are rich in carbonate, whereas in Carboniferous Limestone soils these fractions are generally free of carbonate or, as in 8 out of 20 soils of this type tested, only give a slight reaction with acid.

Mainly as a consequence of the lower clay and higher sand fractions in Carboniferous Limestone soils, the crumb-structure is less stable than in Oolitic soils. The marked difference in stability is readily observed during the grinding of the soil aggregates in the air dried soil.

(vi) <u>Measurement of moisture-retaining properties of the soil.</u>

The soil-moisture constants measured were:-

<u>Hygroscopic coefficient:</u> the amount of water retained by the soil in equilibrium with an atmosphere

of water-vapour of known relative humidity. It represents the amount of water adsorbed on the surface of the soil particles, and therefore gives an indication of the extent of surface active in water-retention.

Permanent wilting percentage: the moisture-content of the soil at which the plant becomes unable to absorb water at sufficient rate to maintain turgor, and it wilts permanently; permanently wilted plants do not recover from wilting when placed in a saturated atmosphere.

Moisture equivalent: the amount of water retained by the soil when 30 gm. of it are subjected to a force of 1,000 x Gravity for 30 minutes (Piper, 1942). For fine-textured soils the moisture equivalent is an approximate measure of the field-capacity, or the amount of water held by the soil under field conditions after the excess water has drained away and the rate of downward movement has materially decreased (Veihmeyer & Hendrickson, 1950).

An approximate estimate of the 'readily available water' (Viehmeyer & Hendrickson, 1950) is obtained by subtracting the permanent wilting percentage from the moisture equivalent.

Methods and results.

Hygroscopic coefficient. (Following the method quoted in Wright, 1939).

8-10 gm. air-dry soil in a shallow nickel dish were exposed, in a vacuumdesiccator, over sulphuric acid solution giving an atmosphere of water vapour of 50% relative humidity. The moisture retained when the soil reached a constant weight gave the hygroscopic coefficient.

Results. The hygroscopic coefficients of 20 soils of each type are summarized in Fig.21.

The majority of Oolitic soils have distinctly higher amounts of hygroscopic moisture (average = 7·70) than most Carboniferous Limestone soils (average = 5·32), indicating that Oolitic soils have a greater extent of soil surface active in water retention. As may be expected the hygroscopic coefficients are very dependent on the amounts of clay and of organic matter in the soil (Figs.22,23, pp.99,100.). Thus six Carboniferous Limestone soils with hygroscopic coefficient greater than 6·0 (soils 15-20, Fig.22) were soils with highest clay and/or organic matter on this limestone; soils with very low hygroscopic values had very low organic matter, though not always low clay.

A similar correlation between amounts of hygroscopic moisture and contents of clay and organic matter is apparent in Oolitic soils (Fig.23).

As there is no conspicuous difference in organic matter content between the two soil types in the 40 samples examined (cf. Fig.19), the marked difference in hygroscopic coefficient is more readily related to the widespread difference in the clay-fractions of the two limestone soils (cf. Fig.20), although differences in the nature of the clay fractions and perhaps also of the organic matter are probably involved. Thus an Oolitic and a Carboniferous Limestone soil of approximately equivalent clay and organic matter contents gave distinctly different hygroscopic coefficients (7·84 and 6·00, respectively).

Moisture Equivalent.

The method of determination followed essentially that described in Piper (1942), except that the technique was modified for use in an ordinary laboratory

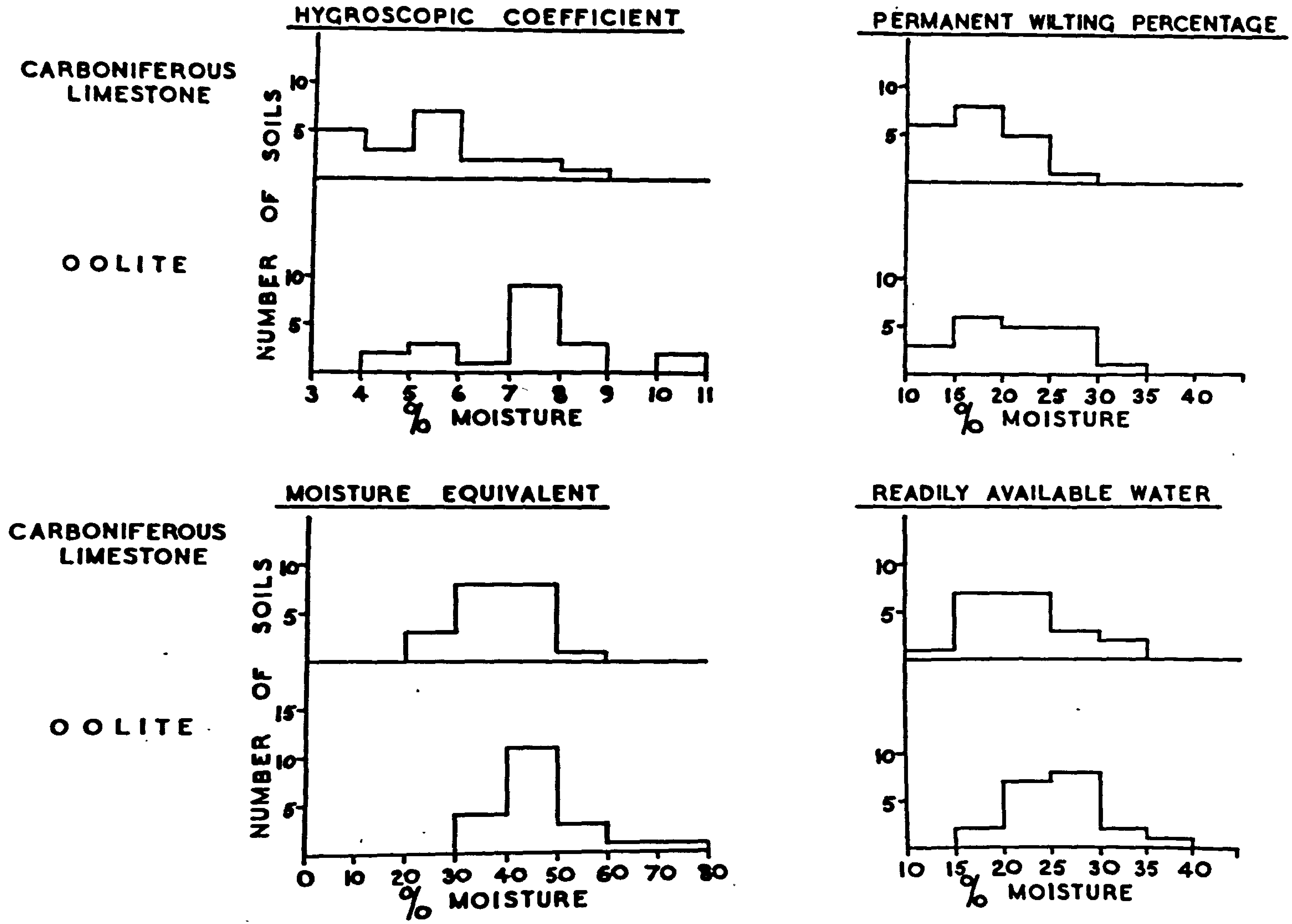


Figure 21. Comparison of moisture-retaining properties for 20 soil samples from each limestone.

centrifuge. In each determination two separate soils, one of each limestone type, were treated simultaneously.

Results. The moisture equivalents of 20 soils of each type are summarized in Fig.21.

In a similar way to the hygroscopic coefficient, the moisture equivalent of the Oolitic soils (average 46%) is distinctly higher than for Carboniferous Limestone soils (average 38%), indicating a generally better water retention in the former soil type.

Moisture equivalent values are correlated with organic matter and clay contents of the soil in much the same way as the hygroscopic coefficient, though the moisture equivalent is not regularly proportional to the hygroscopic moisture (cf. Figs.22,23.).

Permanent wilting percentage.

The procedure used here followed essentially the method described by Briggs & Shantz (1912).

Cress seedlings were grown in zinc pots (2 in. diameter, 2½ in. depth) and, when they were well rooted, the surface of the soil was sealed with a low melting-point grease. The moisture content of the soil when the plants became permanently wilted gave the permanent wilting percentage.

Determinations were made in triplicate for each soil. About 70 gm. air-dry soil were well moistened before transferring to a pot; this permitted normal expansion of the soil on the addition of water without interfering with the porosity of the soil in the pot. The cress plants were allowed to grow until the soil mass was well permeated with roots (about 4-6 weeks); sufficient water was then added to bring the soil moisture content to approximately the moisture equivalent, the cress seedlings were thinned out to approximately 40 plants per pot, and the surface soil was sealed with molten grease (3 parts Vaseline: 2 parts cocoa butter). When the plants were permanently wilted (i.e. when they failed to recover turgor after 3 hours in an atmosphere saturated with water vapour at room temperature), the soil from the lower two-thirds of the pot was freed of cress roots and sampled for drying.

Results. The permanent wilting percentages for 20 soils of each type are summarized in Fig.21.

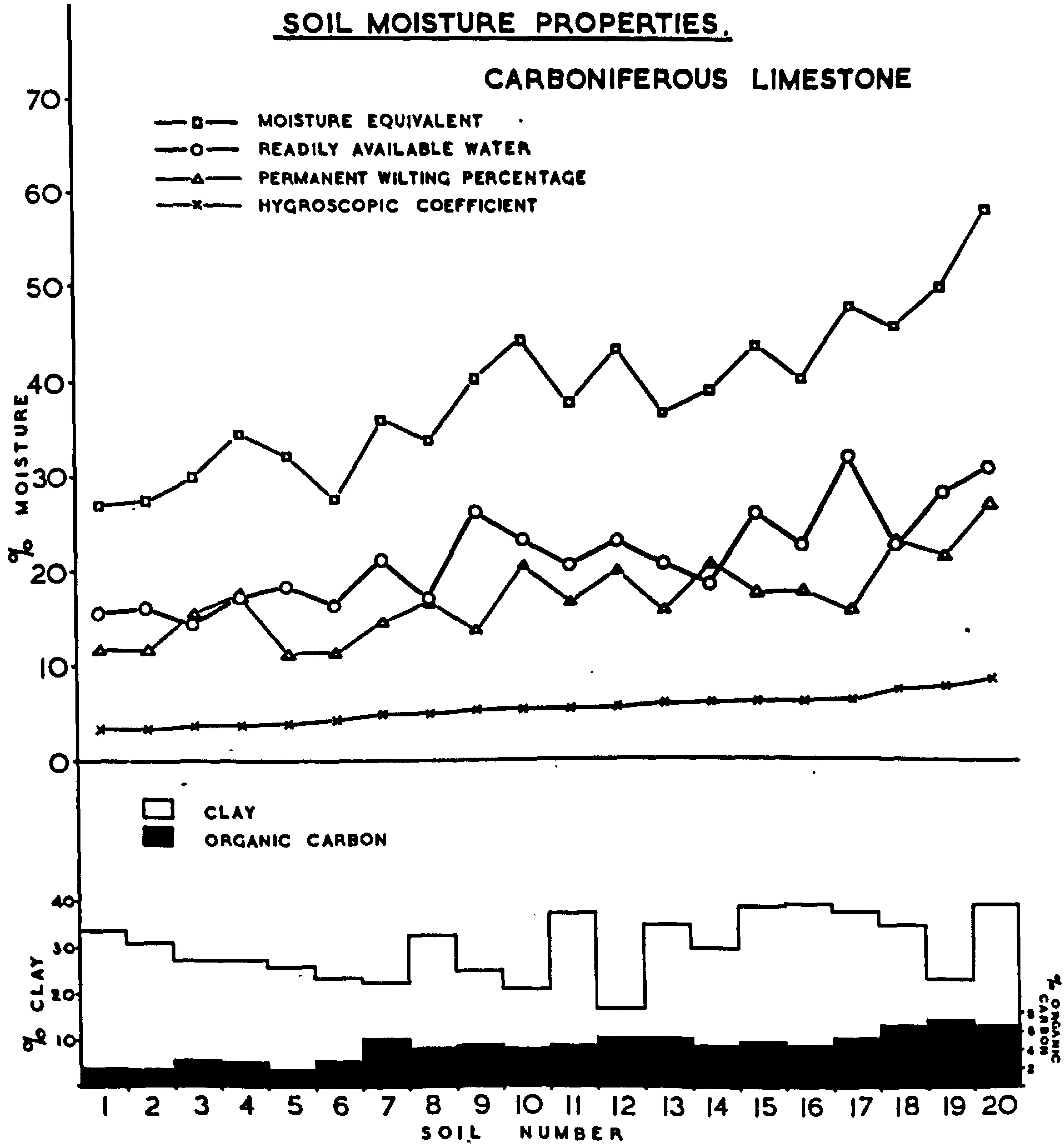


Figure 22. Correlation of moisture-retaining properties in Carboniferous Limestone soils with organic matter and clay contents.

The soil moisture content at the permanent wilting point is generally higher in Oolitic soils; values for this soil type are more frequently high (above 20) and less frequently low (below 15) than for Carboniferous Limestone soils. The average value of the permanent wilting percentage is 21·72 for Oolitic soils and 17·00 for Carboniferous Limestone soils.

As with the other soil moisture constants the permanent wilting percentage is correlated with the physical composition of the soil on both limestones (Figs.22,23.).

Comparison of the times required for the cress plants to reduce the soil moisture content from the moisture equivalent to the permanent wilting percentage revealed no difference in the rate of loss of moisture between the two soil types.

Comparison of the amounts of '<u>readily available water</u>' in the 20 soils of each limestone type (Fig.21.) shows that in general Oolitic soils have larger values (average 25·3%) than Carboniferous Limestone soils (average 21·6%).

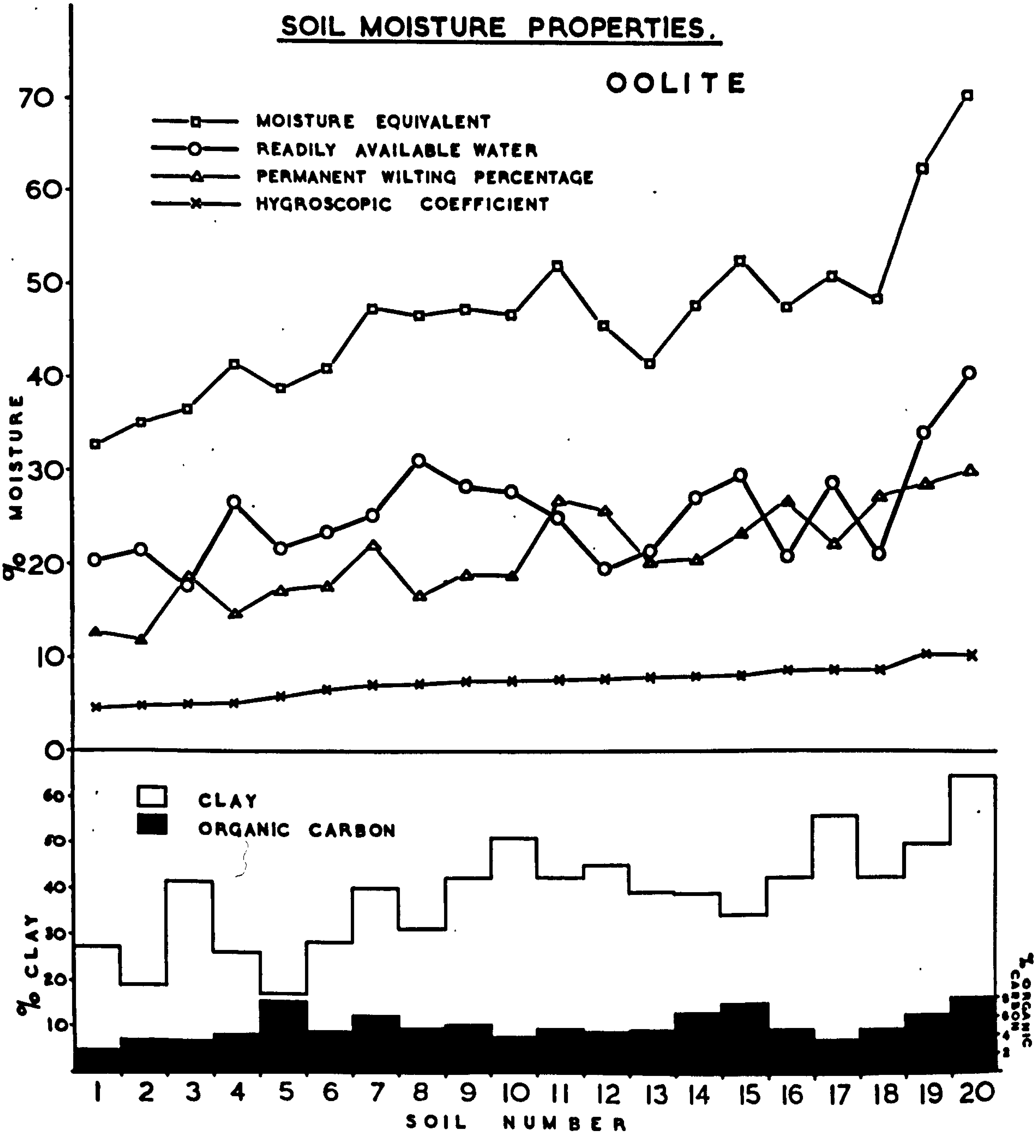


Figure 23. Correlation of moisture-retaining properties in Oolitic soils with organic matter and clay contents.

The higher average amounts of 'readily available water' in Oolitic soils is probably related to the higher clay-contents on this limestone. On both limestones the soils with the highest clay-content generally had the highest values for 'readily availably water', e.g. soil 17, Fig.22; soil 17, Fig.23; though 'readily available water' for some soils is apparently more related to the organic matter content; e.g. soil 15, Fig.23, with high 'readily available water' has relatively low clay but high organic matter, whereas soil 1, Fig.22 and soil 1, Fig.23, with low 'readily available water', have moderate clay but low organic matter. Nevertheless, high organic matter with very low clay values does not generally lead to high amounts of 'readily available water' e.g. soil 5, Fig.23. The highest values for 'readily available water' are shown by soils with high clay and high organic matter e.g. soil 20, Fig.22; soil 20, Fig.23. In a few soils, e.g. soil 9, Fig.22; soil 8, Fig.23, with moderate or low levels of both these components the high 'readily available water' may depend on other soil properties, such as sub-division of the soil-aggregates.

Summary.

The chief differences between the two soil types observed in the laboratory investigation are summarized in the following table:-

TABLE 19

Comparison of the properties of Carboniferous Limestone and Oolitic soils.

Soil property	Carboniferous Limestone	Oolite
pH	Usually 6·5-7·5	Typically higher; usually 7·7-8·1.
Available nutrients:		
Calcium	High levels, but typically very much lower than in Oolitic soils.	Very high; except in four leached soils, where the calcium-levels are similar to typical Carboniferous Limestone soils.
Magnesium	Always high levels.	Usually slightly lower levels.
Potassium	Variable; more frequently high levels.	Variable; more frequently moderate or low levels.
Manganese	More frequently moderate or low levels.	More frequently high levels.
Iron	More frequently very low levels.	Rather more soils with moderately high levels.

Table 19 contd.

Soil property	Carboniferous Limestone	Oolite
Aluminium	Typically low, but some soils with medium levels; one distinctly acid soil (pH= 5·9) showed very high aluminium.	Typically very low; only four leached soils show appreciable aluminium.
Ammonium Nitrate Phosphate	Variable, but similar ranges of levels in the two soil types.	
Texture:-		
Clay	Generally medium clay-content (average = 30%)	Typically high clay-content.
Silt	Low to medium levels; usually higher than in Oolitic soils.	Low to medium levels.
Fine sand	Generally high; non-calcareous.	Typically lower; generally calcareous.
Coarse sand	Typically low; often non-calcareous.	More often high; generally calcareous.
Organic matter	Some soils with very low values; otherwise very similar for the two soil types.	More soils with high values;
Soil moisture constants:-		
Hygroscopic coefficient Moisture equivalent Permanent wilting percentage		Soil moisture constants in general higher in Oolitic soils.
'Readily available water'		Generally higher in Oolitic soils.
	Average = 21·6%	Average = 25·3%

In conclusion of this investigation of soil-characters on the two limestones, it may be said that edaphic conditions on the Oolite are governed by a very dispersed rock-skeleton and a base-saturated soil, such as are typically found in the rendzina type of profile; the base-saturation maintains a good soil structure in the presence of high proportions of clay.

On the Carboniferous Limestone edaphic conditions are governed by a rather sharp demarcation of the soil from the fragmented limestone, both spatially and chemically, such that the soil is normally free of carbonate particles and is typically base-unsaturated, resulting in a profile resembling the terra rossa type. The soil is of a predominantly fine sandy or silty texture. The higher sand and lower clay coupled with the lower base-content, give rise to a less stable soil structure than in Oolitic soil.

V. Experimental measurement of plant growth on the two types.

A simple growth experiment was carried out in which plants were grown in soils of the two limestone-types under identical conditions of cultivation so that the effect of differences between the soils on plant growth could be measured.

Plants of six selected species, showing varying behaviour in the two grassland types were grown on 12 different soils from calcareous grassland (6 each from the Carboniferous and Oolitic limestones), in 6 in. pots in a garden frame; before use, the pots were coated with bitumen on the inside. At the end of the experiment the amounts of plant growth were compared for the two soil types. During the main growing season two of the species were subjected to two different levels of watering treatment.

Experimental Details.

Selection of soils

A preliminary experiment, using a single soil from a typical area on each limestone indicated that differential growth-rates of a given species on the two soil types might be readily related to marked differences in the level of a single plant nutrient in the soil e.g. nitrate. Therefore, to reduce sampling errors of this kind, six different grassland soils from each limestone were used; these were selected to include the major variations in soil conditions encountered on the two limestones.

Soil for the experiment was obtained from the main rooting layer at a number of different points on each grassland area. Each soil was well mixed and sieved through a ½ in. mesh screen before distributing to the pots. Complete analyses of the soils used in the pot experiment are given in the Appendix (p.166).

Species used.

Six species were used; these were of three main types:-

1. Two species which show differential behaviour in the two series of grasslands:

Koeleria gracilis, more plentiful on the Carboniferous Limestone.

Zerna erecta, more plentiful on the Oolite.

These species were grown to test whether their differences of occurrence might be directly related to differences in growth - performance on the two soil types.

2. Two calcicole species, with somewhat similar frequencies of occurrence in the two series of grasslands: Helictotrichon pratense, Helianthemum chamaecistus.

These were grown to test whether a difference of growth - performance on the two soil types is shown by species normally of marked calcicolous habit.

3. Two non-calcicole species with similar frequencies of occurrence in the two grassland types: Festuca ovina, Hieracium pilosella.

These species occur on well - drained soils regardless of calcium - content. They were used as indicators of possible soil - differences which are not directly connected with the calcicolous habit.

Arrangement of soils and species in the frame.

The 12 soils were distributed to 144 flower pots. Each pot contained only plants of a single species. Helictotrichon pratense, Helianthemum chamaecistus, Festuca ovina and Hieracium pilosella, under a single watering treatment, occupied 12 pots each, one pot per individual soil. These numbers were quadrupled for Zerna erecta and Koeleria gracilis; of the 4 pots per individual soil,

Phot. 12. A general view of the growth-experiment (June).

2 were under an adequate watering and 2 under a restricted watering (see below) thus permitting yield - determinations on two separate occasions for each treatment, and giving a total of 48 pots for each species.

Carboniferous and Oolitic Limestone soil types occupied alternate positions in the frame in chequer-board fashion, but, within this arrangement, the positions of individual soils and of the different species on these soils were distributed as randomly as possible. (Phot.12).

Treatment of the plants.

Vegetative shoots were used as starting - material. To ensure genetical equivalence of plants in the two soil types, large vegetative clumps of each species collected from calcareous grassland, were separated into pairs of genetically identical units. Members of such pairs were planted in pots containing respectively a Carboniferous Limestone soil and an Oolitic soil.

Before planting, each shoot was quickly weighed, any surface moisture from washing being removed by lightly pressing between sheets of blotting-paper. A random sample of surplus separated shoots of each species was oven-dried at 80°C, to obtain the average dry weights of the transplanted material.

Shoots were planted in labelled positions, six in a pot; all plants of a species were planted on the same day.

The pots were regularly watered using clear rain water and the frame was ventilated until the plants were fully established. Any casualties and also the plants genetically paired with these, were replaced by fresh plants from time to time. The original planting was in December 1953, and the complete series of plants became fully established at the end of April 1954.

Experimental watering treatment and general cultivation.

As soon as all plants were quite established, the pots containing *Zerna* and *Koeleria* received two levels of watering treatment: a normal or adequate watering treatment similar to that given to the other four species, in which pots received a thorough watering every 3-5 days, and a restricted watering treatment in which the pots were allowed to dry out for several days until the plants showed signs of wilting; the pots were then thoroughly soaked as in the normal watering treatment.

To prevent accidental watering of pots under the restricted watering treatment, the frame was covered whenever there was any risk of rain. A thin coating of a green screening material ('Summer Cloud') on the frame-lights prevented over-heating of the frame during sunny intervals. The surface of the soil in the pots was stirred occasionally to improve aeration.

Measurements of height and spread of each plant, and of number and size of the leaves were made at the beginning of May and again just before the plants were lifted for yield - determinations.

Yield - determinations of Koeleria and Zerna were made during the last week of June and the first week of August 1954. The other four species were harvested during the last week in July. In the yield - determinations, the six plants in a pot were divided from the soil mass, and separately washed, weighed and oven - dried.

Results.

The yield for each individual soil given in Tables 20-27 below, and displayed graphically in Figs. 24-27, represents the combined fresh weight increments of 6 plants in a pot.

In the Tables, horizontally paired figures for the two soil types are from pots containing genetically identical plants.

Increments of dry weight, obtained by subtracting the estimated dry weight of the plants at the time of planting from the final dry weight, are closely proportional to the increments of fresh weight (cf. Fig.25 p.114); and, in general, the trends shown in comparisons of dry weight data are similar to those shown by fresh weight data, but are sometimes less marked (cf. Fig.25). In the experiment fresh weight data have been preferred since they seemed likely to give a more accurate measure of the effective bulk of the plants.

The significance of the mean difference of growth - increment between the two soil types has been tested for each species, using the 't' test quoted by Brownlee (1949, page 32). The corresponding values of probability (P) are given at the end of each table.

For *Koeleria* and *Zerna*, only the results of the second sampling (August) are given; in the first sampling, (June) the trends of growth for both species, although less marked, were very similar to those in the later sampling.

Koeleria gracilis.

Progress of growth.

Moderately easily established after transplanting; plants showed repeated tillering and some increase in length of the leaves. The appearance of the plants at the end of the experiment was very similar on the two soil types except that on Oolitic soils the leaf number was generally greater. Plants with a restricted water - supply, though similar for the two soil types, were much smaller than those with an adequate water - supply.

Plant yield data. (Second sampling.)

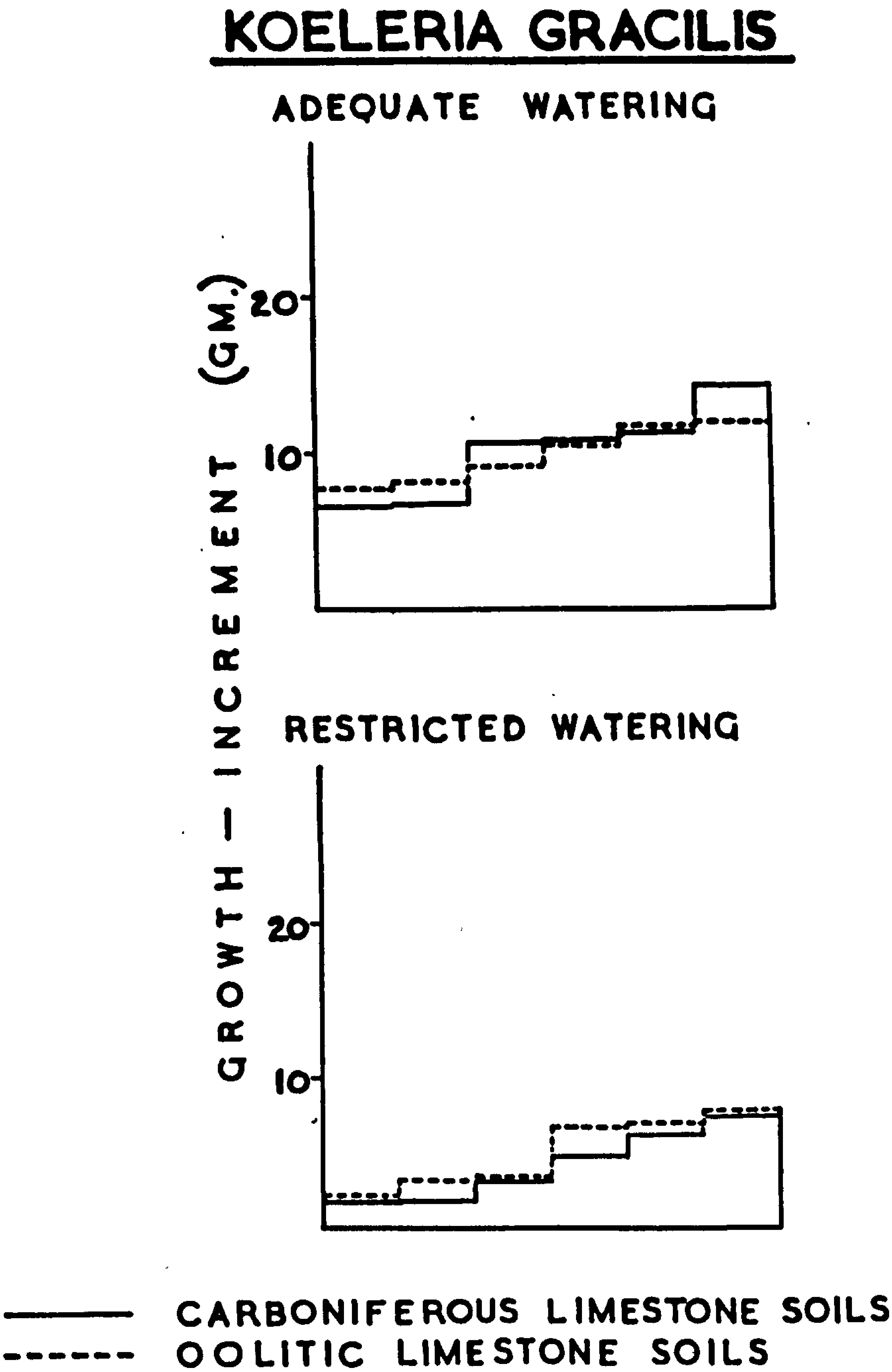


Figure 24. Comparison of the growth-increments of *Koeleria gracilis* on the two soil types. Fresh weight data for six soils of each limestone type (Table 20 .p.112.) arranged in ascending order of growth-increment.

TABLE 20 (cf. Fig.24)

Koeleria gracilis - Increase in fresh weight (grams)

Carboniferous Limestone		Oolitic Limestone		
Soil No.	Fresh wt. increment	Soil No.	Fresh wt. increment	Difference between the two soil types
a) Adequate watering				
1	6·658	10	7·922	− 1·264
3	10·577	8	10·548	+ 0·029
4	6·851	6	9·179	− 2·328
5	11·339	9	11·654	− 0·315
7	10·877	12	8·223	+ 2·654
11	14·347	2	11·903	+ 2·444
			Mean difference:	+ 0·203
		P	lies between 0·9 and 0·8	
b) Restricted watering				
1	1·878	2	3·036	− 1·158
3	6·053	6	6·927	− 0·874
4	1·794	9	2·114	− 0·320
5	4·780	10	7·620	− 2·840
7	7·378	12	6·630	+ 0·748
11	3·062	8	3·268	− 0·206
			Mean difference:	0·775
		P	lies between 0·2 and 0·1	

It is evident that the growth - rates of Koeleria are very similar on the two soil types under both watering treatments, though there are slight indications that with an adequate water - supply, Carboniferous Limestone soils on average produce better growth; there is more pronounced evidence of better growth in Oolitic soils when the water - supply is restricted.

Zerna erecta

Progress of growth

Not always readily established after transplanting; some of the older, coarse vegetative shoots did not readily form fresh roots. There was a steady growth-rate throughout the experiment; some plants formed inflorescences (one per plant) on Oolitic soils 23/144 plants (16%) produced inflorescences, compared with 12/144 (8%) on Carboniferous Limestone soils. In the plants without flowers, there was a considerable elongation of leaves and a slow increase in leaf - number. The appearance of the plants was similar on the two soil-types, though on some Carboniferous Limestone soils, especially under the adequate watering - treatment, Zerna often appeared more vigorous (more tillers and greater leaf - number). Considering both soil-types, plants generally appeared somewhat more vigorous under the adequate watering treatment.

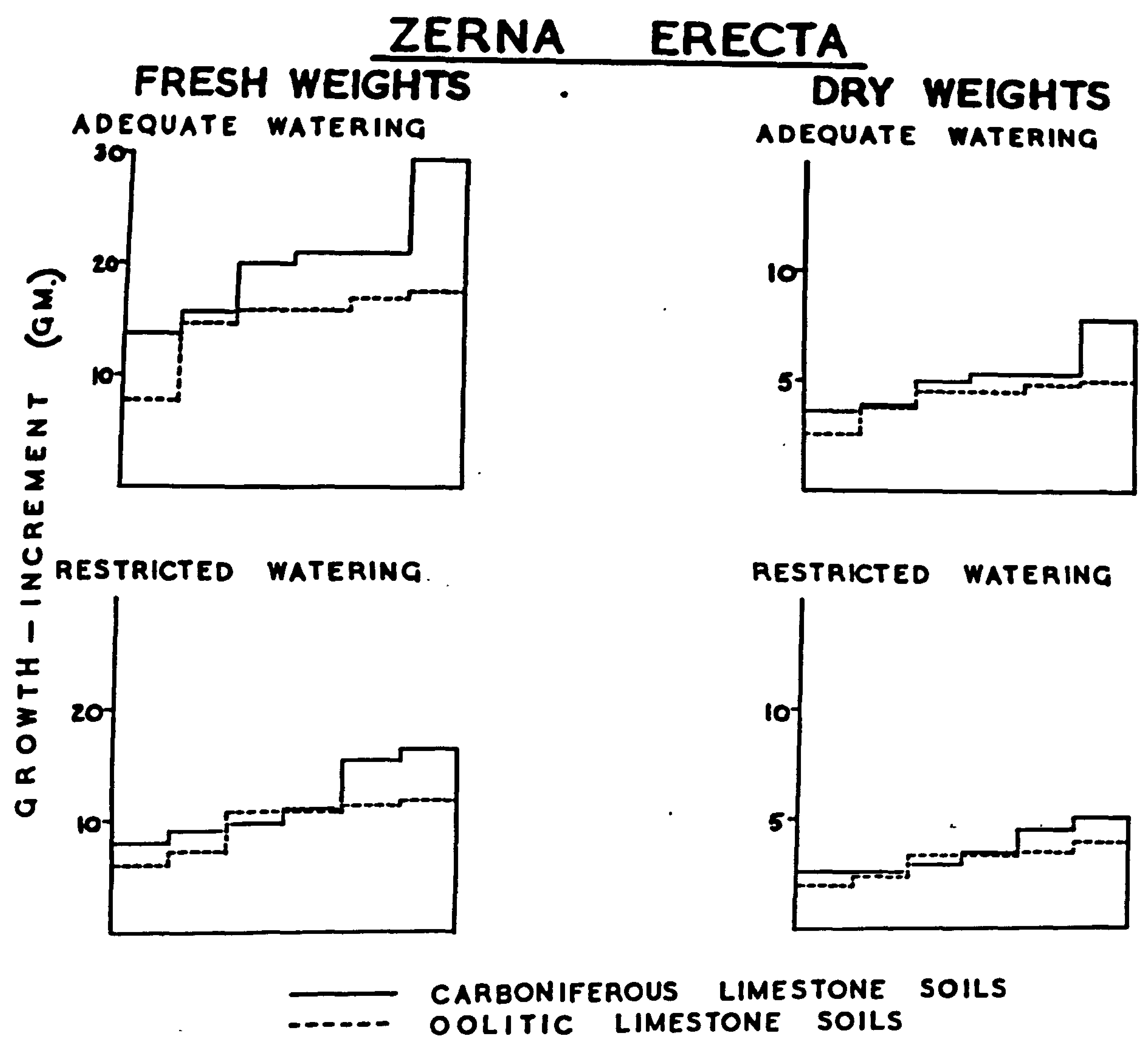


Figure 25. Comparison of the growth-increments of Zerna erecta on the two soil types.Data for six soils of each limestone type (fresh weights,Table 21 ,p.114) arranged in ascending order of growth-increment.

TABLE 21 (cf. Fig.25)

Verna erecta - Increase in fresh weight (grams)

Carboniferous Limestone		Oolitic Limestone		
Soil No.	Fresh wt. increment	Soil No.	Fresh wt. increment	Difference between the two soil types
a) Adequate watering				
1	15·726	9	15·809	− 0·077
3	21·062	2	7·706	+ 13·356
4	21·089	6	15·892	+ 5·197
5	13·753	8	15·956	− 3·203
7	29·538	12	14·549	+ 14·989
11	20·044	10	17·555	+ 2·489
				Mean difference: + 5·458
			P lies between 0·2 and 0·1.	
b) Restricted watering				
1	9·747	6	11·017	− 1·270
3	15·482	9	11·815	+ 3·667
4	16·496	2	6·094	+ 10·402
5	7·992	10	10·742	− 2·750
7	11·085	8	7·389	+ 3·696
11	9·033	12	11·476	− 2·443
				Mean difference: + 1·883
			P lies between 0·5 and 0·4	

There is a strong indication that with an adequate water-supply the growth rates of _Zerna_ are higher in Carboniferous Limestone soils. With a restricted water-supply there is only a slight indication of higher growth-rates of _Zerna_ in Carboniferous Limestone soils.

The variations of fresh weight increment within the two soil types are not simply related to any soil - property, but in Carboniferous Limestone soils with a restricted water-supply there is a correlation between the growth - increment of _Zerna_ and the amount of 'readily available water' in the soil (Table 22; Fig.26).

TABLE 22.

Soil No.	'Readily available water'	Growth - increment of _Zerna_
11	15·58	9·033
5	18·43	7·992
1	18·44	9·747
7	23·39	11·085
3	26·49	15·482
4	31·82	16·496

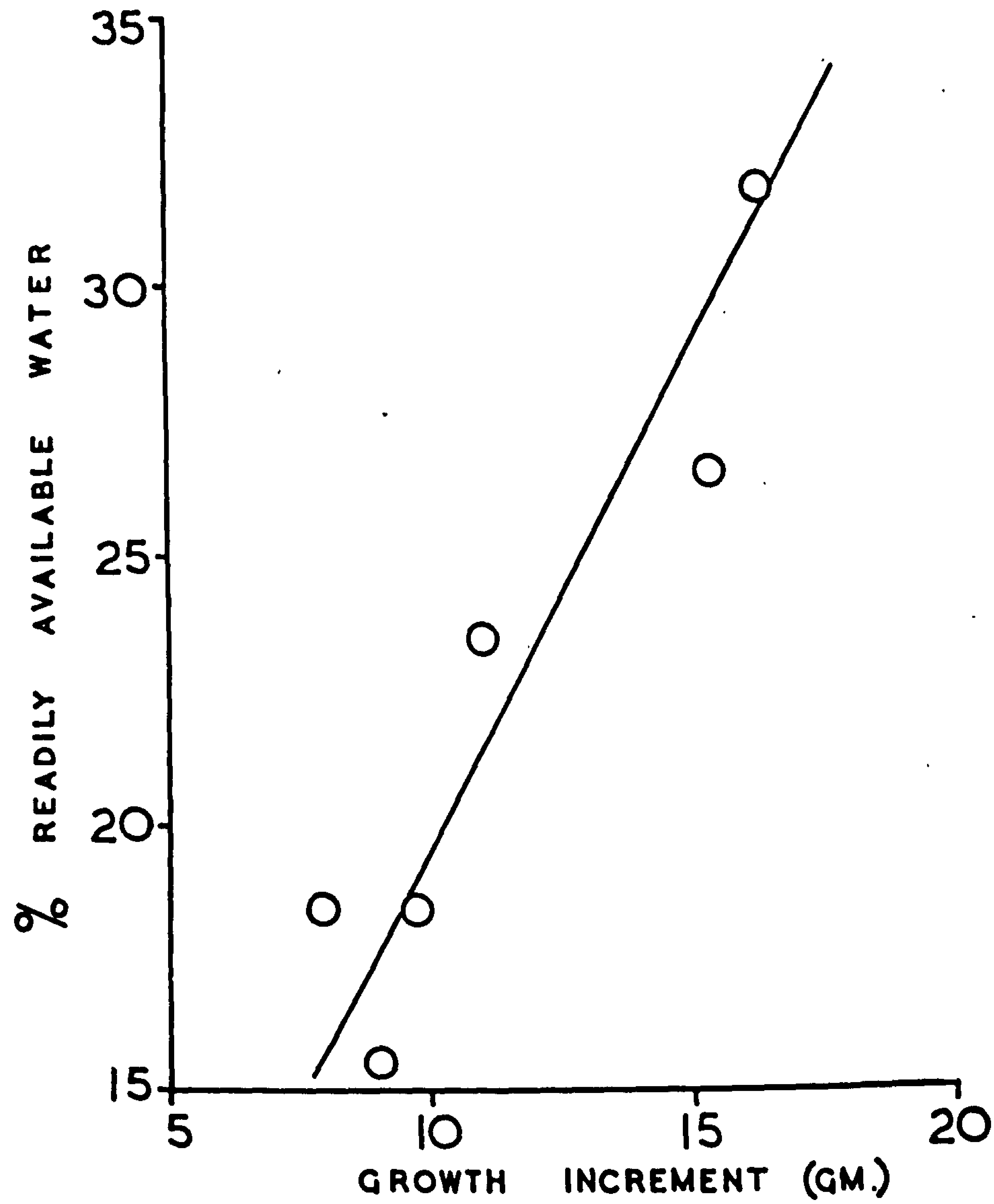


FIGURE 26. Correlation of the growth-increment of <u>Zerna erecta</u> with 'readily available water' in Carboniferous Limestone soils under a restricted watering treatment.

Thus under conditions of restricted water supply the amount of plant growth may be very dependent on the 'readily available water' in the soil.

Helictotrichon pratense

Progress of growth.

Readily established after transplanting; plants showed a very steady increase in size and number of leaves, with considerable tillering. Plants were of very similar appearance on the two soil types though on Oolitic soils, shoots were generally more branched and carried more leaves.

Plant yield data.

TABLE 23 (cf. Fig.27)

Helictotrichon pratense - Increase in fresh weight (grams)

Carboniferous Limestone Soil No.	Fresh wt. increment	Oolitic Limestone. Soil No.	Fresh wt. increment	Difference
1	13·680	8	12·972	+ 0·708
3	7·617	12	11·524	- 3·907
4	13·441	10	21·413	- 7·972
5	8·498	2	10·273	- 1·775
7	6·832	6	8·042	- 1·210
11	10·350	9	16·416	- 6·066

Mean difference: -3·370

P lies between 0·1 and 0·05.

These results practically establish that the growth rate of *Helictotrichon* is higher in Oolitic soils than in Carboniferous Limestone soils, under the conditions of the experiment.

Helianthemum chamaecistus

Progress of growth

Transplanted shoots were very difficult to get established; because of this difficulty growth on most soils was uniformly poor. Where growth was appreciable plants appeared more vigorous on Oolitic soils.

Plant yield data.

TABLE 24 (cf. Fig.27)

Helianthemum chamaecistus - Increase in fresh weight (grams)

Carboniferous Limestone Soil No.	Fresh wt. increment	Oolitic Limestone. Soil No.	Fresh wt. increment	Difference between two soil types
1	− 0·100	9	1·743	− 1·843
3	0·783	12	1·946	− 1·163
4	0·605	8	0·066	+ 0·539
5	1·589	2	2·395	− 0·806
7	− 0·439	10	0·067	− 0·506
11	− 0·457	6	0·178	− 0·635

Mean difference: − 0·735

P lies between 0·1 and 0·05

Very few *Helianthemum* plants produced appreciable fresh growth; on some Carboniferous Limestone soils there was an overall loss in fresh weight. The general trend of increase in fresh weight of the plants indicates that Oolitic soils on average produce somewhat better growth than Carboniferous Limestone soils.

Two Oolitic soils with high clay (soils 2,12) produced the highest growth increments.

Festuca ovina

Progress of growth.

Readily established after transplanting; plants showed repeated tillering, and on some soils, a marked elongation of the leaves. The range of size and appearance of the plants was very similar on the two soil types.

Plant yield data.

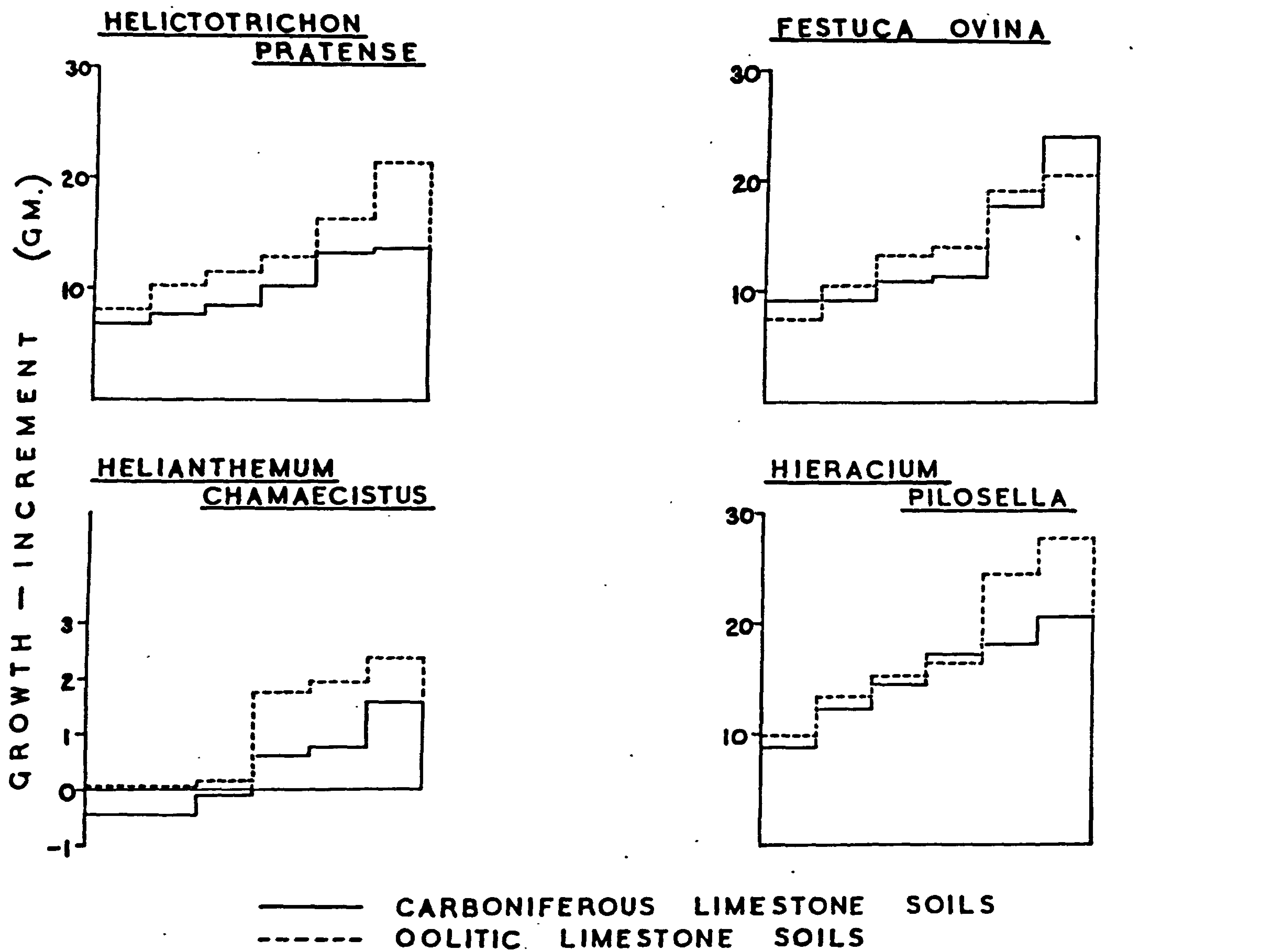


Figure 27.Comparison of growth-increments on the two soil types. Fresh weight data for six soils of each limestone type (Tables 23- 26;pp.117-123)arranged in ascending order of growth-increment.

TABLE 25 (cf. Fig.27)

Festuca ovina - Increase in fresh weight (grams)

Carboniferous Limestone Soil No.	Carboniferous Limestone Fresh wt. increment	Oolitic Limestone Soil No.	Oolitic Limestone Fresh wt. increment	Difference between two soil types
1	11·409	2	13·333	− 1·924
3	9·146	6	20·658	− 11·512
4	11·071	9	7·466	+ 3·605
5	9·019	8	10·504	− 0·485
7	17·874	12	14·096	+ 2·778
11	24·085	10	19·085	+ 5·000

Mean difference: − 0·423

P lies between 0·9 and 0·8

It is apparent that F. ovina exhibits a similar range of growth-rates on the two soil types, though there is some indication that growth is a little better on Oolitic soils.

The performance of Festuca in this experiment gives an indication of the striking qualitative differences which may be displayed in trials of this kind. Festuca plants in

Carboniferous Limestone soil 11 had yellowish-green leaves while all plants on other soils, including plants genetically identical to those in soil 11, had dark green leaves.

It is unlikely that the growth - increments or appearance of F. ovina on the different soils are related to any single soil property. However it may be noted that soil 11 differs appreciably from the other Carboniferous Limestone soils used in the experiment only in its moderately high levels of available aluminium and of phosphate. In the Oolitic soil type four soils containing moderately high levels of available iron (produced relatively high growth increments) while the remaining two Oolitic soils, with lower levels of iron showed lower growth increments.

Hieracium pilosella

Progress of growth.

Fairly readily established after transplanting; on most soils, the plants showed a fairly rapid growth, with increases in size and number of leaves and a considerable branching of the rosettes, with the formation of trailing shoots. There was a fairly widespread formation of inflorescences. From a total of 36 plants on each soil type, inflorescences were formed as follows:-

	No. of plants flowering	Total no. of inflorescences formed
Carboniferous Limestone	23	23
Oolitic Limestone	27	33

The vigour of the plants varied considerably amongst individidual soils although there was a similar range of appearance in the two soil types; in general Oolitic soils produced somewhat more vigorous plants.

Plant yield data.

TABLE 26 (cf. Fig.27)

Hieracium pilosella - Increase in fresh weight (grams).

Carboniferous Limestone		Oolitic Limestone.		
Soil No.	Fresh wt. increment	Soil No.	Fresh wt. increment	Difference between two soil types
1	14·489	2	15·372	− 0·883
3	12·340	6	9·970	+ 2·370
4	17·356	9	16·498	+ 0·858
5	20·633	12	24·492	− 3·859
7	18·035	8	13·431	+ 4·603
11	8·789	10	27·706	− 18·917

Mean difference:- − 2·638

P lies between 0·5 and 0·4

It is apparent that the growth-rates of H. pilosella are similar on the two soil-types though there are indications that the Oolitic type produces slightly better growth.

Summary and conclusions.

Although the soils of the two limestones differ markedly in a number of properties (summarized on page 101.), they produce no very striking differences in the growth-rates of the species tested. The following table summarizes the main results:-

TABLE 27

Comparison of the growth-behaviour of the selected species on the two soil types.

Species	Watering Treatment	Comparative growth-behaviour	
		Carboniferous Limestone soils	Oolitic Limestone soils
Koeleria gracilis	Adequate	Growth a little better than on Oolitic soils	——
	Restricted	——	Growth better than on Carboniferous Limestone soils
Zerna erecta	Adequate	Distinctly higher growth-rates.	Lower growth-rates but more inflorescences produced.
	Restricted	Slightly higher growth-rates	
Helictotrichon pratense	Adequate	——	Significantly higher growth-rates
Helianthemum chamaecistus	"	——	Growth better
Hieracium pilosella	"	——	Growth somewhat better. More inflorescences produced.
Festuca ovina	"	Very similar growth-rates on both soil-types	

The most consistent differences in soil conditions to which any general growth differences between the two soil-types may be related, are those of pH and of levels of available calcium. It seems from the results of the growth experiment that properties such as texture, which are variable within each soil type, do not often exert a marked influence on growth-rate. Thus for a single limestone type, soils with high clay content only occasionally produced growth-amounts markedly different from other soils of the same type, e.g. Zerna, under restricted watering, showed relatively low growth-rates on Oolitic soils 2 and 8, with high clay.

Unknown soil-properties, perhaps differing characteristically between the two soil-types e.g. the constitution of the clay fraction or of the organic matter, may also have affected the plant growth-rates. However, the available information indicates that with adequate watering the growth-rates of Zerna erecta and, to a lesser extent, of Koeleria gracilis are higher in the approximately neutral pH and the relatively low calcium levels characteristic of Carboniferous Limestone soils. On the other hand the growth of Helictotrichon pratense, and to some extent that of Helianthemum chamaecistus, *Hieracium pilosella* and *Festuca ovina* are more favoured by the high pH and very high calcium of Oolitic soils.

With a restricted watering treatment the growth rates of *Koeleria* and *Zerna* on Oolitic soil compare more favourably with those on Carboniferous Limestone soils; thus for *Zerna* the growth-differences between the two soil-types were less marked with the restricted watering, while the growth of *Koeleria* is better on Oolitic soils under these conditions, compared with a better growth on Carboniferous Limestone soils with adequate watering. The higher amounts of 'readily available water' in Oolitic soils may be of importance under dry soil conditions in enhancing the growth-rates of plants such as *Koeleria* and *Zerna* on this soil type, compared with Carboniferous Limestone soils.

From the comparison of inflorescence - production in *Hieracium pilosella* and *Zerna erecta* on the two soil types it would seem that the Oolitic soils are the more favourable to ~~influence~~ inflorescence development in these species, under the conditions of the experiment. The possibility that this result is a consequence of an uneven distribution of shoots with differentiated inflorescence primordia at the time of planting seems unlikely, because of the large number of plants involved and the random method of selection of these for the two soil types.

VI. DISCUSSION

The calcareous grasslands of the Carboniferous and Oolitic Limestones of the Bristol region are superficially similar grassland communities; but the results of a detailed examination of these grasslands (Section III) reveal a number of characteristic and widespread differences in floristic composition. The more important of these have been discussed at the end of Section III (pp.40-51).

There is strong circumstantial evidence that the differences between the grasslands have arisen to a large extent from differences in soil conditions on the two limestones. The distinct floristic composition of each type of grassland is retained over a wide geographical area and in a large number of different situations, embracing a considerable range of climatic, topographical and other environmental influences. For example, on the Carboniferous Limestone, grassland in the areas with relatively high Mean Annual rainfall is of essentially similar character to that in the areas of lower rainfall. It would seem, therefore, that edaphic conditions represent the predominant influence giving rise to the distinctive characters of the two series of grasslands.

The chief differences in soil conditions of the grasslands on the two limestones, revealed in the detailed soil investigations (Section IV), are those of pH and levels of available calcium, with other less consistent, but often well-marked differences in texture, water-retaining properties and in the levels of some plant nutrients. (Table 19, pp.101-102).

The ph and levels of available calcium have relatively much lower values in Carboniferous Limestone soils compared with typical Oolitic soils, and there is direct evidence that these differences between the two soil types have been of primary importance in determining the differential behaviour of a number of species on two limestones.

The normal habitats of the species in Table 9 (p.45) listed as 'exclusive to the Carboniferous Limestone' (e.g. Calluna vulgaris, Erica cinerea, Agrostis canina are on very acid soils, so that their frequent presence on the Carboniferous Limestone (8,9,4 times respectively) and their complete absence on the Oolite appears to be directly related to the more marked tendency towards leached soil conditions on the former. Furthermore the general occurrence on the Carboniferous Limestone of other species (included in Table 9) normally associated with acid soil conditions, and the very infrequent presence of these species in Oolitic grassland is almost certainly related to the lower pH and much lower levels of calcium in Carboniferous Limestone soils. Evidence that this is so is provided in the floristic composition of leached areas on the Oolite. Four such areas, for which soil data are available, bear a number of the species listed in Table 9 at appreciable levels of abundance (cf. Table 28); the pH and calcium-levels of the soils from these areas are much lower than normal for the Oolite and are comparable with those of typical Carboniferous Limestone soils.

TABLE 28

The occurrence of 'acidic' species on the Oolite in relation to soil properties.

Columns 1-4: Levels of abundance on four leached soils.

Column 5: Frequencies of occurrence on sixteen soils with high carbonate.

	1	2	3	4	5
Agrostis tenuis	f	f	f	o	8
Potentilla erecta	-	o	-	o.lf	-
Sieglingia decumbens	-	r	a.lva	f	-
Veronica officinalis	-	r	-	-	-
Viola riviniana	-	r	-	f	-

The last four species in Table 28, occurring on leached Oolitic soils, are normally absent from Oolitic grassland, but, on the other hand, are fairly characteristic on the Carboniferous Limestone (occurring on 22,47,22, 12, out of 50 areas, respectively). Their presence as conspicuous members of limestone grassland in this region appears, therefore, to be directly associated with low pH and relatively low levels of calcium in the soil.

Agrostis tenuis occurs at moderate levels of abundance on a variety of Oolitic soils with high carbonate-content, so that its presence in grassland is not primarily dependent on the low pH and low calcium of leached soils; but as Agrostis tenuis is more characteristic of the Carboniferous Limestone, it may be favoured by these conditions.

From the observed behaviour of Sieglingia decumbens on the Oolite, there is little doubt that its occurrence is favoured by leached soil conditions. Five out of the total of seven occurrences of Sieglingia on the Oolite were on areas showing evidence of leaching; on these areas Sieglingia often showed moderately high levels of abundance. It was recorded as 'rare' on the remaining two areas, with soils rich in carbonate. From this distinctive behaviour of Sieglingia it seems reasonable to relate its greater success on the Carboniferous Limestone to the relatively low pH and calcium-levels of the soils on this rock-formation. This view is in agreement with widespread observations of the behaviour of _Sieglingia._

However, from the distribution of this species on the Chalk it seems that the presence of _Sieglingia_ may not always primarily depend on low pH and low calcium; thus, although a common member on leached Chalk soils, it occurs in abundance on carbonate-rich soils of the Chalk in several regions of south-west England (Hope-Simpson, unpublished data).

As was noted in the discussions of the soil profiles (p.74) the relatively low calcium-content of Carboniferous Limestone soils, and with it probably the low pH, depend very much on the manner of weathering of the parent rock. The non-dispersal of rock-fragments and the hard, homogeneous nature of the limestone limits the release of calcium into the soil.

However, there are indications that base-retention in Carboniferous Limestone soils is also restricted by the nature of the clay. Since the soil profile on the Carboniferous Limestone resembles the terra rossa profile, it seems likely that the soil on this limestone would show the terra rossa character of a relatively low clay - silica: sesquioxide ratio (about 2); it also seems probable that the clay of Oolitic soils has a relatively high silica: sesquioxide ratio (about 4) characteristic of rendzinas (Robinson, 1949). A low silica: sesquioxide ratio indicates that the clay is mainly of the kaolinitic type, whereas values around 4 are associated with a montmorillonite type of clay. The latter type has an expanding crystal-structure, and consequently has a higher base-exchange capacity and a greater degree of hydration than the kaolinitic type, which has a fixed crystal lattice (Baver, 1948). It therefore seems likely that the rendzina soils of the Oolite contain a more base-retentive clay than Carboniferous Limestone soils.

There is some evidence in support of this supposition. In a Carboniferous Limestone soil examined which had a moderately high content of dispersed and readily soluble calcium content, albeit of artificial origin, the soil component freed of lime particles does not contain carbonate nor is the available calcium higher than in other Carboniferous Limestone soils. In most Oolitic soils the soil freed of limestone particles is rich in carbonate and shows very high levels of available calcium.

The apparently better base-retaining properties of Oolitic soils act in addition to the influence of the dispersed carbonate in making soils on the Oolite less susceptible to reduction to a low base-content. Thus it may be said that under exactly similar pedogenic forces the equilibrium condition in the soil on the Carboniferous Limestone is more strongly tending towards a low base-content than in Oolitic soil.

A manifestation of this is readily observed in the field. On the Oolite the great majority of areas have soils with a high content of calcium carbonate and high pH, and showing no signs of leaching. There is evidence of a lowering of pH and of calcium-levels only where the soil is very far removed from the parent rock, as in the deep soils on a few gentle slopes or plateau sites, or in some of the rather deep clay soils on moderately sloping land. On the Carboniferous Limestone the soil only retains a moderately high pH and levels of calcium where erosion is very active and the soil very close to the parent rock, as on the steepest and driest slopes; as soon as any appreciable depth of soil is built up, e.g. on less steep slopes or moister situations, the calcium-content and pH are rapidly lowered.

The extent of the leaching process on Carboniferous Limestone varies with local conditions; it is increased with greater soil-depth, moister aspect and higher rainfall. For example, on a southern slope at Crook Peak, where rainfall is relatively low for the Carboniferous Limestone, the vegetation is predominantly calcicolous and the soil pH is relatively high (7·92); further inland in the Cheddar Head region where rainfall is considerably higher, a site of similar aspect and with similar soil depth carries conspicuous amounts of non-calcicolous flora, including *Potentidla erecta* and *Veronica officinalis*, and the soil has a lower pH (6·88).

In view of the marked physiological effect which the differences in pH and calcium-level between the two soil types are likely to have on plant growth, these differences may be expected to have some influence in determining the differential behaviour of plants other than those depending primarily on leached soil conditions. There is however no direct evidence of this in the floristic composition of leached Oolite areas.

Furthermore it was not possible on either limestone to correlate trends in other soil properties with features of the vegetation-cover. Thus there was no direct evidence from the observed data that the fairly general differences in texture, moisture-retention and in the levels of some nutrients between the two soil types, have been important in producing any of the vegetation differences of the two series of grasslands. However, it seems reasonable to suppose that the different trends in these more variable soil properties on the two limestones have had some effect on the differences in the vegetation-cover. For example, although Oolitic soils in general have distinctly higher powers of moisture-retention, apparently arising from the usually higher clay-contents, moisture of direct importance to plant growth ('readily available water'), is not very significantly higher, compared with Carboniferous Limestone soils; but these slight differences may lead to an advantage for plants on the Oolite during prolonged dry spells. Since the greater exposure of the Carboniferous Limestone grasslands to wind-action probably leads to a more rapid lowering of soil-moisture through higher transpiration-rates, the significance of such an advantage may be considerably increased.

Although the only direct evidence available for a dependence of grassland differences between the two limestones on soil conditions concerns the differences of pH and calcium-levels, it is possible that floristic differences may have depended on characteristic soil differences not revealed in the investigations described in Section IV. For example, the physical organization of the soil appears from handling to be characteristic for each limestone type, even when comparing soils with very similar mechanical composition. It is known that the sand fractions of the two soil types are of different chemical character (p.93) and it has been indicated previously (p.103) that the differences in base-saturation between the two soil types lead to differences in stability of the soil aggregates. Furthmore, there are indications of fundamental differences in the constitution of the clay in the two soil types and, considering the characteristic differences of soil colour, probably of the organic matter also; there is some indirect evidence of such constitutional differences apparent when correlating soil moisture properties with mechanical composition (p.96).

Thus a more complete knowledge of the properties of Carboniferous and Oolitic Limestone soils may be necessary before the effects of edaphic differences on floristic behaviour in the two series of grasslands can be fully assessed. From the indications referred to in the preceding paragraph it would seem that the characteristic differences between the two soil types are fundamentally chemical. On this account an indirect expression of these differences might be reasonably expected in the levels of available plant nutrients in the soil.

The results of Morgan tests (pp.101,102), besides providing clear evidence of the very different levels of available calcium in the two soil types, show some evidence of different trends in the levels of other elements. This is most marked in the levels of aluminium: it is probable that the higher aluminium of Carboniferous Limestone soils is associated with the lower pH, since the aluminium level in leached Oolite soils is higher than normal. The differences noted in the available levels of other elements (magnesium, potassium, manganese, iron) may arise from the different levels of calcium in the two soil types or these may be an expression of differences in the parent material of the soil.

The results of the Morgan tests, however, must be interpreted with caution, since the conditions of extraction may affect the two soil types differentially inasmuch as Oolitic soils are highly buffered with calcium carbonate, while Carboniferous Limestone soils are carbonate-free.

The results of the growth experiment (Section V) may be interpreted as agreeing in some measure with the evidence from the field-observations that the differences between the soils of the two limestones have not markedly influenced the differences in the vegetation. None of the species tested showed very marked growth-differences on the two soil types.

However, a number of interesting growth-features were shown:

For the calcicole species _Helianthemum chamaecistus_ and _Heliototrichon pratense_, there was rather pronounced evidence of better growth on soils from the Oolite; it could be reasonably supposed that the highly calcareous soils of this limestone are more favourable to the growth of markedly calcicole species. Nevertheless two other species grown: _Koeleria gracilis_ and _Zerna erecta_, normally regarded as calcicoles, showed indications of higher growth rates in Carboniferous Limestone soils. This result resembles that of Webb & Hart (1945) who found that seedlings of a number of species, including calcicoles showed better growth in acid soil. The decreased advantage of the Carboniferous Limestone soils over Oolitic soils in promoting the growth of _Zerna_ and _Koeleria_ under restricted watering, may arise from the lower retention of soil moisture in Carboniferous Limestone soils, particularly of 'readily available water'.

The fairly similar growth-rates shown on the two soil types by the two non-calcicole species of similar behaviour on the two limestones (Hieracium pilosella, Festuca ovina) support the view that the two soil types do not differ markedly except in properties connected with the calcicole habit. Thus, in the light of the normally accepted distribution of the plants tested, the results (except for Koeleria and Zerna) confirm the field-observation that the soil differences of greatest effect on the vegetation are those of pH and calcium-levels, and that these are only important when considering plants of marked calcicole tendencies.

It is however probable that the small growth-differences observed in the experiment will be of competitive significance under natural conditions; but it may also be expected that these will be to a greater or lesser extent modified by the operation of other environmental factors. This seems clearly demonstrated when the results of the growth experiment are considered in relation to the behaviour of the species tested in the grasslands of the two limestones.

Thus _Zerna_, with somewhat better growth-rates on Carboniferous Limestone soils, would apparently be better able to compete on this soil type than on Oolitic soils. However the existing floristic composition indicates that the reverse is true. The weaker competitive power of _Zerna_ on the Carboniferous Limestone soil type is perhaps illustrated by the following example: on a very rocky slope in a sheltered situation on the Carboniferous Limestone, _Zerna_ was very abundant where the soil was shallow and other species were sparse, but was absent on scattered packets of somewhat deeper soil bearing the normal complement of grassland species. It is possible that, compared with growth on Oolitic soils other species show a proportionately higher growth rate than _Zerna_ on Carboniferous Limestone soils, such that ultimately _Zerna_ can compete better on the Oolite. The evidence from the growth-rates of the other species tested in the growth experiment e.g. _Heliototrichon pratense_ is against this possibility since growth was better on Oolitic soils. It therefore seems more likely that the growth rate of _Zerna_ under natural conditions is very much influenced by other environmental influences not present in the conditions of the experiment e.g. wind-action and competition from surrounding plants.

In spite of the higher growth rates of _Helianthemum_ and _Helictotrichon_ on Oolitic soils, _Helianthemum_ shows similar behaviour on the two limestones (Table 4 p.34) and _Helictotrichon_ occurs more frequently and more abundantly on the Carboniferous Limestone (Table 2b p.29). A possible reason for the similar behaviour of _Helianthemum_ on the two limestones has already been given (p.47). The growth-rate of _Helictotrichon_ may be reduced in Oolitic grassland by the relatively taller herbage.

The results of the growth-experiment for _Hieracium pilosella_ and _Festuca ovina_ are not at variance with the behaviour of these two species in the field. Both species show fairly similar growth-rates on the two soil types and both have similar frequencies of occurrence in the two series of grasslands. The higher levels of abundance of _Festuca_ on the Carboniferous Limestone (Table 4-6,) are probably a consequence of the shorter herbage heights on this limestone.

The slightly better growth of <u>Koeleria</u> on soils from the Carboniferous Limestone with adequate watering is in agreement with its greater frequency of occurrence and greater abundance on this limestone.

Thus it is apparent when edaphic factors are isolated from the environmental complex that differences between the soils of the two limestones do not produce very marked differences in plant growth for the species tested. The most significant growth differences observed, which seem most readily related to the characteristic soil differences of pH and calcium-content, only concern species, e.g. <u>Helictotrichon pratense</u> of strongly calcicolous behaviour.

From the results of the growth-experiment and soil-investigations, correlated with the observed behaviour of species in the field, the evidence suggests that other environmental influences have a predominant effect over edaphic conditions for species other than those very sensitive to differences of pH and calcium-content of the soil.

The following are illustrations, for some of the species grouped at the end of section III, of the probable operation of other environmental factors leading to a differential behaviour on the two limestones:

a) _Zerna erecta_. The problem of the distribution of _Zerna erecta_ is of special interest in the comparison of the calcareous grasslands of the Carboniferous and Oolitic Limestones. From its observed behaviour in the two series of grasslands, three main environmental influences seem to be important in determining its distribution:

1. _Carbonate content of the soil._ The general correlation of the universal occurrence of _Zerna_ on the Oolite with the usually high content of carbonate in soils on this limestone, is borne out by the occurrence of _Zerna_ as a dominant on a Carboniferous Limestone soil (at Draycott), where there is a large content of free carbonate particles from an artificial liming. Several other sites on Carboniferous Limestone, with soils of relatively high available calcium for this limestone, show small amounts of _Zerna_. However, _Zerna_ occurs at moderately high levels of abundance on a relatively acid soil (pH 6·1) on the Carboniferous Limestone, and it is also abundant on the Oolite where the soil is leached and free of carbonate,

so that its occurrence is not primarily determined by the carbonate content of the soil. This is also indicated by a parallel behaviour of *Zerna* in Central Germany and in Switzerland, where it occupies siliceous and even acid soils as well as being a regular member on soils of high pH (Wilczek *et al*., 1928, Klapp, 1931; quoted from Hope-Simpson, 1940).

2. *Shelter from wind action.* The occurrence of *Zerna* seems to be favoured by sheltered conditions. Most grassland areas on the Oolite, characteristically bearing *Zerna* at high levels of abundance, are in sheltered situations, and all the Carboniferous Limestone areas bearing this species are totally or partially sheltered; three of these where *Zerna* is 'dominant' or 'very abundant', are unusually sheltered for the Carboniferous Limestone. The morphology of *Zerna* may be important in determinining its preference for sheltered areas: with its tall habit and coarse leaves, *Zerna* may be at a disadvantage in very exposed situations. However, *Zerna* is present as a dominant on some of the very exposed grassland areas on the Oolite, e.g. Cleeve Hill, so that exposure to wind is not an absolute limiting factor in the distribution of this

species.

3. Intensity of grazing. There is little doubt that the success of *Zerna* is favoured by light grazing. All the areas bearing this species on the Carboniferous Limestone were ungrazed, or only lightly grazed in recent years. On the Oolite, it was very often dominant where there was little or no grazing, whereas it occurred at reduced levels of abundance on some of the heavily-grazed areas; however it appears to be tolerant of moderately heavy grazing by cattle on this limestone, especially when the soil is shallow and competition from other species is less severe. On the Chalk (Hope-Simpson, 1940b), a dominance of *Zerna* is associated with relaxed grazing conditions, whereas this species is suppressed and may be at length eradicated by heavy grazing.

Although the grazing intensities on the Carboniferous and Oolitic Limestones are apparently similar at the present time (p.56), there are indications of past grazing differences. The gradual change from pastoral to a arable farming accompanying the decline in the wool trade, and perhaps also the general recession of agriculture in the

1930's, probably affected grazing on the two limestones in different ways. In the largely unenclosed rough grazings of the Mendips, though the intensity of grazing decreased with the decrease in livestock population, there were probably no discontinuities of grazing. On the other hand, many grassland areas on the Oolite, being privately owned, may have experienced sharp discontinuities in grazing treatment and perhaps were completely neglected for a number of years. Such irregularities of grazing are almost certainly favourable to a widespread establishment of Zerna erecta (and also of Brachypodium pinnatum, discussed below). This difference in grazing on the two limestones may have been an important contributory factor to the differential occurrence of both Zerna and Brachypodium.

The marked tendency for the development of Zerna and Brachypodium in Oolitic grasslands when grazing is restricted was observed by Lees (1867); this tendency therefore, appears to be a long established characteristic of these grasslands.

The chief environmental influences apparently determining the distribution of Zerna erecta in the two series of grasslands may be summarized: Zerna is favoured by a high carbonate-content of the soil, sheltered site-characters and a light grazing-intensity. However, it may tolerate the lack of one of these principle conditions providing the other two are sufficiently pronounced. Thus on the Carboniferous Limestone Zerna occurs on a leached soil when in a sheltered, lightly-grazed situation. It is present on the Oolite in very exposed situations where the soil has excess carbonate and the herbage is ungrazed; or, as in a number of Oolitic areas, where the soils have high carbonate and the sites are sheltered, but grazed. It is noteworthy that on a quite exposed, well-grazed Oolitic plateau site with leached soil, Zerna is present at a relatively low level of abundance for Oolitic grassland (recorded as 'frequent'); nearby on the same area where the soil was shallow above the limestone, Zerna was 'very abundant'.

Since high free carbonate of the soil and sheltered site-characters are characteristic on the Oolite but occur rarely on the Carboniferous Limestone, and since also past grazing may have been less regular on the Oolite, it may be concluded that these factors are the most important in determining the much greater abundance of _Zerna_ in Oolitic grassland.

b) The distribution of _Brachypodium pinnatum_, widespread and characteristic on the Oolite, may be governed by somewhat similar factors to that of _Zerna erecta_. Thus on the Carboniferous Limestone, where it is normally absent _B. pinnatum_ is of conspicuous occurrence on the Draycott area, where the soil contains free carbonate and the site is sheltered and ungrazed. However, this species is dominant on a Mendip plateau site at Crook Peak where the soil is acid; it also occurs abundantly on both exposed and grazed areas on the Oolite.

It seems clear that _B. pinnatum_ is very readily established under light grazing conditions; but afterwards it may be relatively immune to long periods of heavy grazing. The present distribution of _Brachypodium_ probably depends to a large extent on the past grazing history of individual areas. This species is of very infrequent occurrence on the southern Cotswolds, where farms are small and grazing has been relatively intense and continuous but it is of universal occurrence on the grasslands of the northern Cotswolds, where past grazing has probably been much less regular. The difference of occurrence of B. pinnatum on the two series of grasslands has probably arisen in a similar manner to that of Zerna, but for Brachypodium the grazing factor has probably been of much greater importance.

c) As suggested previously (p.42), the difference in herbage heights in the two series of grasslands may be an important factor leading to the differential occurrence of the species included in Tables 7 and 8 (pp.42,43). The taller herbage on the Oolite, arising mainly from the widespread occurrence of Zerna erecta and Brachypodium pinnatum must selectively favour tall-growing species on this limestone; whereas the infrequency of Zerna and Brachypodium or of any other tall-growing species on the Carboniferous Limestone favours short-growing species.

The different trends of floristic composition apparently arising from the differences in herbage-height are probably emphasized by the greater exposure to wind-action of grassland sites on the Carboniferous Limestone. The dwarfing influence of the wind is often very pronounced on this limestone.

d) The differential occurrence of the species classed as 'agricultural' (Table 10, p.46) appears to have arisen chiefly from differences of the 'seed dispersal pressure' of these species on the two limestones.

On the Oolite where farming is more intensive (cf. p.14), areas of calcareous grassland are much nearer to land under regular agricultural treatment; recorded grassland areas were very frequently situated within fields well-stocked with cattle, and many areas were adjacent to arable land. On the Carboniferous Limestone, though a number of recorded areas were under routine farm grazing, these were in general only recently developed as farmed land; by far the majority of areas form part of a large expanse of sparsely-stocked rough grazings, and are relatively remote from regularly farmed land. Very few oolitic areas are in comparable situations. Hence the dispersal pressure of many of the species in Table 10 is very much greater in the calcareous grasslands of the

Oolite.

Thus in the examples of differential species-behaviour quoted above (a-d,) other environmental influences appear to have prevailed over the edaphic differences between the two limestones.

VII. SUMMARY

1. A comparative survey of calcareous grassland has been made on the Carboniferous Limestone centred in the Mendip Hills, Somerset, and on the Oolitic Limestone of the Cotswold Hills, Gloucestershire.

2. On the Carboniferous Limestone the majority of calcareous grassland areas are in rough grazings, but are confined to regions where the soil is shallow. On the Oolite the distribution of semi-natural calcareous grassland is hardly dependent on soil depth, but is practically restricted to steep slopes, because of ploughing elsewhere.

3. The floristic composition of these grasslands has been described using the method of subjective estimation. Flora lists from 50 areas of each type of grassland are summarized and compared in tabular form. The great majority of species recorded are common to both limestones, but many of these show a different behaviour in the two grassland types.

Oolitic grassland characteristically contains *Zerna erecta*, generally in great abundance and often in association with Brachypodium pinnatum. These species are of very limited occurrence in Carboniferous Limestone grassland, where Fescues and low-growing herbs dominate the herbage. A number of species characteristic of acid soils are of very general occurrence on the Carboniferous Limestone, whereas these species are restricted to a very few leached areas on the Oolite. Tall-growing species and species associated with agricultural treatment are relatively more frequent on the Oolite.

4. It is clear that edaphic conditions differ characteristically on the two limestone outcrops; other environmental factors e.g. rainfall, may show locally distinct differences between the two limestone regions but these are not consistent over the whole areas of outcrop.

The edaphic conditions beneath grassland on the two limestones have been described in detail. The soil profile on Carboniferous Limestone resembles the terra rossa type: the soil is reddish-coloured, carbonate-free, and sharply separated from the parent rock. The Oolitic soil profile is a rendzina: the soil is brown or dark brown, carbonate-rich and full of fragmented parent rock. The profile differences are related to differences in rock structure between the two limestones.

5. Soil analyses were made on composite samples from 20 representative grassland areas on each limestone. The two soil types differ most characteristically in pH and calcium-levels: Oolitic soils have typically high pH and very high levels of available calcium, Carboniferous Limestone soils have lower pH and much lower calcium-levels, characters shared by leached Oolitic soils.

Oolitic soils generally have distinctly higher clay-contents, and consequently better powers of water-retention, and Carboniferous Limestone soils have generally higher contents of fine sand and silt. 'Readily available water' is, on average, higher in Oolitic soils.

6. An experiment is described in which six grassland species of varying behaviour on the two

limestones were grown in soils of the two limestone types under identical conditions of cultivation. Two grasses: Zerna erecta, Koeleria gracilis were grown with different watering treatments.

There were no great differences of growth on the two soil types for any of the species tested. Two marked calcicoles, Helianthemum chamaecistus and Helictotrichon pratense, occurring with approximately similar frequencies of occurrence on the two limestones, produced somewhat better growth on Oolitic soils under the experimental conditions. Zerna erecta characteristic and abundant on the Oolite, showed distinct indications of better vegetative growth on Carboniferous Limestone soils under both watering treatments. Under conditions of drying out of the soil, the growth of Zerna erecta and Koeleria gracilis on Oolitic soils compares more favourably with that on Carboniferous Limestone soils than when the water-supply is adequate.

7. An abundance of Zerna erecta appears from field-observations on both limestones to be related to a high carbonate-content of the soil, sheltered

site-characters and a light grazing treatment, factors much more typical of the Oolite.

8. The relation of differences in floristic composition of the two series of grasslands to edaphic differences is discussed. There is clear evidence that the differences of occurrence on the two limestones of species common on acid soils are associated with the characteristic soil differences of pH and calcium-levels. The results of the growth-experiment support the view that differences in soil properties connected with the calcicole habit have the most marked effect on the differences in floristic composition. In the differential behaviour of the great bulk of the species it seems that other environmental influences have been at least as important as edaphic conditions.

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Appendix Table 1

Analyses of soil samples from 20 areas of calcareous grassland on the CARBONIFEROUS LIMESTONE.

a) Locations of areas sampled.

Soil sample	Location of grassland area	Map reference
A	S.E. slope, Compton Hill.	31 / 393559
B	S. slope, Shute Shelve Hill, near Axbridge.	31 / 425551
C	S. slope, above Cheddar.	31 / 454546
D	S. slope in valley, near Charterhouse.	31 / 486548
E	S. slope, near Priddy.	31 / 516493
F	Gentle S. slope, Dolebury Warren.	31 / 453589
G	N. slope, Dolebury Warren.	31 / 451592
H	Steep rocky S. slope, Dolebury Warren.	31 / 450587
J	S. slope, Goblin Combe.	31 / 476653
K	S. slope, Tickenham Hill.	31 / 445724
L	S. slope, Middle Hope.	31 / 324659
M	E. slope, Loxton Hill.	31 / 369561
N	S.W. slope, Winscombe Hill.	31 / 414554
P	Grazed plateau site, Shute Shelve Hill.	31 / 429556
Q	S.E. slope, above Cheddar.	31 / 463553
R	S. slope, near Cheddar Head Farm.	31 / 505529
S	S. slope, above Draycott.	31 / 487515
T	Gentle S. slope, Rookham.	31 / 542485
U	N. slope, Dulcote Hill.	31 / 567444
V	S.E. slope, Worminster Sleight.	31 / 578431

b) **Analyses.** (Carboniferous Limestone soils).

Soil Sample	Pot Expt. Soil.No.	pH	Mechanical analysis Clay	Silt	Fine Sand	Coarse sand	Organic carbon
A	1	6·60	25·98	18·48	33·78	15·76	1·97
B	5	7·58	29·59	21·63	38·24	1·88	4·55
C	7	6·81	20·74	25·74	39·88	1·82	4·01
D	3	6·68	24·74	28·47	37·46	2·06	4·49
E	4	6·42	37·63	19·14	29·69	1·39	5·32
F	11	6·59	33·81	16·52	45·15	2·85	1·99
G		6·87	27·63	20·12	42·42	3·04	2·84
H		7·35	34·65	22·22	23·04	10·89	5·17
J		7·46	30·82	20·33	46·00	2·76	1·94
K		7·54	23·14	19·87	23·19	17·82	7·10
L		7·88	23·39	8·13	24·53	38·67	2·97
M		7·77	38·38	23·81	28·06	5·39	4·98
N		7·90	16·56	24·35	35·10	12·91	5·10
P		6·36	34·75	30·88	29·75	0·83	6·69
Q		6·10	27·62	28·68	38·48	2·57	3·00
R		6·86	22·10	33·28	39·40	3·19	5·16
S		8·04	32·04	21·70	36·56	3·92	4·09
T		5·81	37·20	34·69	24·18	2·41	4·35
U		7·31	39·37	23·59	22·51	1·83	6·60
V		7·63	38·69	25·42	29·86	1·33	4·48

Analyses (contd.) (Carboniferous Limestone soils).

Soil Sample	Hygroscopic coefficient	Moisture equivalent	Permanent wilting percentage	'Readily available water'.
A	3·90	32·25	13·81	18·44
B	5·79	38·90	20·47	18·43
C	5·23	44·12	20·73	23·39
D	5·23	40·29	13·80	26·49
E	6·28	47·65	15·83	31·82
F	3·31	27·18	11·60	15·58
G	3·73	34·59	17·26	17·33
H	5·67	36·53	15·82	20·71
J	3·35	27·63	11·53	16·10
K	7·69	49·74	21·53	28·21
L	4·24	27·71	11·36	16·35
M	5·97	43·44	17·47	25·97
N	5·45	43·23	20·13	23·10
P	7·33	45·48	22·69	22·79
Q	3·60	30·04	15·53	14·51
R	4·88	35·87	14·67	21·20
S	4·93	33·81	16·73	17·08
T	5·33	37·81	16·97	20·84
U	8·52	58·00	27·05	30·95
V	6·00	40·01	17·54	22·47

Appendix Table 2

Analyses of soil samples from 20 areas of calcareous grassland on the OOLITE.

a) Locations of areas sampled.

Soil sample	Location of grassland area.	Map reference
A	S.E. slope near Marshfield.	31 / 763742
B	N.W. slope near Marshfield.	31 / 776756
C	S. slope near Cold Ashton.	31 / 764732
D	S. slope near N. Wraxall.	31 / 819760
E	S. slope near N. Wraxall.	31 / 832766
F	S. slope near Biddestone.	31 / 846734
G	S.W. slope, Lansdown.	31 / 711685
H	S. slope, W. Yatton Down, Castle Combe.	31 / 853761
J	S.W. slope, Burton.	31 / 824796
K	S. slope, Broad Hill, Hawkesbury.	31 / 768863
L	S.E. slope, Wotton-under-Edge.	31 / 776944
M	S.W. slope, near Nailsworth.	31 / 837973
N	N.W. slope, near Tetbury.	31 / 908945
P	S. slope, Barnsley Wold, near Cirencester.	42 / 065077
Q	Gentle N. slope, Barnsley Wold, near Cirencester.	42 / 064074
R	N.W. slope, Ablington Downs, near Bibury.	42 / 099087
S	W. slope, near Eastington.	42 / 140123
T	W. slope, near Eastleach.	42 / 179076
U	S. slope, near Burford.	42 / 237095
V	Plateau site, Upper Slaughter.	42 / 141235

b) Analyses. (Oolitic soils).

Soil Sample	Pot Expt. Soil No.	pH	Mechanical analysis Clay	Silt	Fine sand	Coarse sand	Organic carbon
A	10	7·71	26·19	33·29	22·00	7·92	4·11
B	12	7·73	42·49	28·48	15·70	3·31	4·86
C	2	7·55	51·58	19·64	20·48	2·02	3·95
D	6	7·88	19·03	20·86	26·32	26·57	3·57
E	9	7·78	31·64	18·32	17·08	20·36	4·91
F	8	7·84	42·36	16·33	19·25	11·10	4·85
G		7·78	64·84	14·23	7·27	1·00	8·01
H		7·96	34·10	16·95	17·20	19·10	7·45
J		7·68	27·26	13·33	26·30	20·94	2·38
K		7·61	40·26	19·06	20·69	12·14	6·20
L		8·00	17·07	16·38	18·06	37·02	7·81
M		6·89	55·82	17·58	23·91	0·48	3·63
N		7·00	42·50	23·25	24·93	1·53	5·21
P		8·00	39·31	18·98	22·68	10·47	4·64
Q		7·06	45·62	21·39	26·77	0·61	4·47
R		7·62	49·96	14·76	20·80	4·22	6·21
S		8·08	38·73	14·47	31·86	5·16	6·57
T		8·04	41·87	7·41	29·52	13·79	3·34
U		7·90	28·49	18·46	22·51	21·99	4·37
V		7·40	42·11	14·88	31·72	3·64	4·76

Analyses (contd.) (Oolitic Limestone soils).

Soil Sample	Hygroscopic coefficient	Moisture equivalent	Permanent wilting percentage	'Readily available water'.
A	5·15	41·46	14·59	26·87
B	7·67	51·97	26·96	25·01
C	7·63	46·73	18·83	27·90
D	4·91	35·05	13·58	21·47
E	7·29	46·78	16·56	30·22
F	8·65	48·32	27·26	21·06
G	10·28	70·53	30·04	40·49
H	7·93	52·58	23·18	29·40
J	4·61	32·72	12·52	20·20
K	7·09	47·31	22·08	25·23
L	5·91	38·99	17·16	21·83
M	8·61	50·73	22·06	28·67
N	7·45	47·35	18·90	28·45
P	7·84	41·63	20·21	21·42
Q	7·74	45·61	25·83	19·78
R	10·28	62·53	28·47	34·06
S	7·81	47·69	20·47	27·22
T	5·06	36·45	18·50	17·95
U	6·45	41·13	17·64	23·49
V	8·45	47·48	26·63	20·85

APPENDIX TABLE 3

pH and available nutrients in the growth-experiment soils.

Soils sampled early in (March).

Carboniferous Limestone soils.

Soil No.	pH	Morgan test readings. NO_3	NH_4	PO_4	K	Ca (10xdil.)	Mg	Mn	Al	Fe
1	7·69	10	1	4	10	4	10	1	2	2
3	7·10	8	2	1	8	2	10	1	4	1
4	6·96	10	4	4	8	6	10	2	2	1
5	7·74	10	1	6	10	2	10	2	2	1
7	7·10	10	1	4	10	2	10	4	2	2
11	7·84	8	1	10	6	4	10	6	6	1

Oolitic Limestone soils.

Soil No.	pH	NO_3	NH_4	PO_4	K	Ca (10xdil.)	Mg	Mn	Al	Fe
2	8·01	10	1	1	8	10	10	10	1	4
6	7·97	10	1	1	6	10	8	8	1	10
8	7·95	10	1	1	6	10	8	6	1	1
9	8·10	10	1	2	4	10	8	8	1	1
10	8·08	10	1	1	8	10	8	10	1	4
12	8·01	10	2	1	10	10	8	10	1	2

Memorandum prescribed by regulations.

1. The investigations recorded in this thesis are the results of my own independent work. The research was supervised throughout by Dr. J.F. Hope-Simpson, who suggested the problem and who has greatly assisted in its investigation by critical discussion, and in the recording of a few grassland areas.

One series of soil extractions for Morgan tests was made in the laboratories of the National Agricultural Advisory Service, S.W. Region.

2. In this research the semi-natural calcareous grasslands occurring on the Carboniferous and Oolitic Limestones of the Mendip and Cotswold Hills are described comparatively. The soil conditions beneath these grasslands have been studied in detail, and floristic differences on the two limestones are related as far as possible to soil differences. A pot experiment was performed to assess the effect on plant growth of the differences between the soils of the two limestones.

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